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Established Predators of *Fiorinia externa* Ferris (Hemiptera: Diaspididae) on Eastern Hemlock (*Tsuga canadensis* (L.) Carriere) in Urban and Forest Sites

Christine Ann Lynch
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a thesis written by Christine Ann Lynch entitled "Established Predators of *Fiorinia externa* Ferris (Hemiptera: Diaspididae) on Eastern Hemlock (*Tsuga canadensis* (L.) Carriere) in Urban and Forest Sites." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Entomology and Plant Pathology.

Paris Lambdin, Major Professor

We have read this thesis and recommend its acceptance:

Jerome Grant, Kevin Moulton, Rusty Rhea

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Abstract

A project was initiated in September 2004 to determine the indigenous predators of *Fiorinia externa* Ferris, the elongate hemlock scale (EHS), on eastern hemlock and their impact on the pest populations. Branch samples were taken monthly from four sites (two forest and two urban) in eastern Tennessee and western North Carolina to assess predator damage from October 2004 to April 2006. Predators of this exotic pest were collected from beat sheet samples from September 2004 to May 2006. Laboratory tests were conducted from field-collected predators to assess food consumption, feeding behavior, and intraguild competition among predators of EHS. From field samples, the average predator damage was 8.28% (range 4.72 to 9.84%) for the four sites, and predator damage was found throughout the year. Six predaceous species (*Chilocorus stigma, Harmonia axyridis*, *Rhyzobius lophanthae, Scymnillus horni*, *Scymnus loweii*, and *Conwentzia pineticola*) were documented to feed on EHS. There were 346 total adult predators, one pupa, and 157 larvae collected from September 2004 through May 2006. *Rhyzobius lophanthae* was the only predator collected throughout the year. The highest numbers of specimens collected were from the urban sites. *Chilocorus stigma*, *R. lophanthae*, and *S. horni* had the highest EHS consumption rates. From the functional tests, *S. horni*, *R. lophanthae*, and *C. stigma* exhibited different searching patterns for recognizing EHS as prey. *Chilocorus stigma* had the shortest prey recognition times, while *R. lophanthae* had the longest prey recognition times. *Scymnus loweii* did not feed during the functional tests. When four of the predators were tested in different combinations, all four exhibited aggressive tendencies, and this territorial behavior could cause feeding disruption. *Rhyzobius lophanthae* and *S. horni* consumed fewer *Adelges tsugae* females or immatures compared to EHS and were more prey specific. In fecundity tests, *R. lophanthae* most commonly laid eggs singly on a branch, needles, side of Petri dish, or filter paper than in clusters. It also laid eggs near or under EHS exuviae. Based on consumption and seasonal abundance, *R. lophanthae*, *C. stigma*, and *S. horni* should be further evaluated for use as biological control agents to complement the parasitoid, *Encarsia citrina*. (348 words)

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I. Literature review

Tsuga (hemlocks)

Worldwide, ten species of hemlocks comprise the genus *Tsuga*, four of which are native to North America with two eastern, *Tsuga canadensis* and *Tsuga caroliniana*, and two western species (Fig. 1.), *Tsuga heterophylla* and *Tsuga mertensiana* (Fowells 1965). The other six species are found in temperate parts of Asia including the Himalayas, China, Taiwan, and Japan. Morphologically, the bark of these trees is deeply furrowed and cinnamon-red, the branches are asymmetrically horizontal to drooping, the shoots are slender, and the buds are rounded and not resinous. The leaves are needlelike, flattened, arranged in two rows, and rounded or notched at the end. In the spring, male and ovulate strobili are produced on the same tree from buds formed the prior year. The male strobili occur at the leaf bases, and female cones occur on the terminal end of the leaves. The small female cones are ovoid or cylindrical in shape, hang downward, mature over one season, and remain attached until the following year. There are three to six cotyledons, and each rounded cone scale has a pair of long-winged seeds at the base (Fowells 1965).

Tsuga canadensis (L.) Carriere

Importance

Eastern hemlock, *Tsuga canadensis* (L.) Carriere, is a late successional tree that provides a unique and more constant habitat than other areas of the forest (Finzi et al. 1998, Fuller 1998, Orwig and Foster 1998, Danoff-Burg and Bird 2002). This tree has been a component of northeastern forests in the United States since the Holocene. Its microclimate attracts several species of birds, plants, and fish (McClure et al. 2001, Mitchell 1999, Danoff-Burg and Bird 2002). Streams surrounded by hemlocks are the preferred habitat for native brook trout because of lower water temperatures, and a temperature elevation of 6 to 9° C when the hemlocks were removed (Lapin 1994).

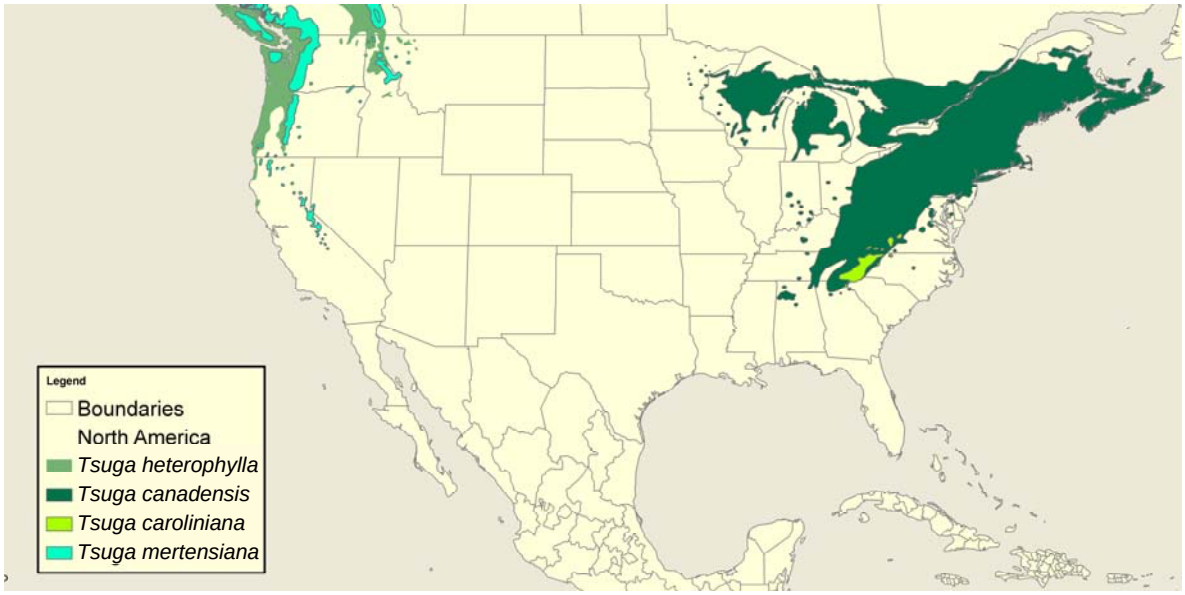

Fig. 1. Range of the four North American *Tsuga* species.

These trees also are important to tourism in state and national forest parks because of the aesthetic qualities generated by their presence (Royle and Lathrop 1997, Danoff-Burg and Bird 2002). The Great Smoky Mountains National Park contains about 35,399 ha of eastern hemlock at different elevations, and forests comprised of hemlocks provide recreational opportunities, beautiful waterfalls, historic structures, and diverse flora and fauna (Buck et al. 2005). The possible extensive mortality of eastern hemlock would have considerable ecological and socioeconomic impact (Royle and Lathrop 1997, Danoff-Burg and Bird 2002).

Habitat conditions

Eastern hemlock is most productive in humid and cool areas with adequate moisture present during all seasons (Thornthwaite 1948). The length of the growing season for these trees ranges from 80 days or less in the north to 200 days along the Atlantic coast and southern United States (Fowells 1965). It produces a dense canopy when in groups or stands and creates a cooler and moister microclimate than other hardwood stands of a similar age in the same area (Daubenmire 1931, Friesner and Potzger 1932, 1934, 1936, 1944; Hough 1945, Moore et al. 1924, Oosting and Hess 1956, Shreve 1927). *Tsuga canadensis* grows in many different soil conditions including shallow rocky soils or extremely acidic soils in the eastern United States and Canada (Hough 1942, Hough 1943, and McClure 1977b). Throughout most of its range, eastern hemlock is found in podzolic, brown podzolic, and gray-brown podzolic zonal soil groups (Fowells 1965). It also occurs on shallow soils such as peat and muck and half-bog soils of Maine, the Lake States, and Canada. In the extreme southern parts of its range, it is found on gray-brown podzolic, lithosols, and red and yellow podzolic lateritic zonal soil groups of the Appalachians (Fowells 1965). For areas with below optimum climate conditions, hemlocks will be found only in moist and cool valleys, northern and eastern slopes, coves, benches, sides of ravines, or hollows under cliffs (Frothingham 1915, Jennings 1927, Shreve et al. 1910).

Eastern hemlock is a major component of four forest types, which are Type 22 with white pine - hemlock, Type 23 with hemlock, Type 24 with hemlock - yellow birch,

and Type 58 with yellow-poplar - hemlock. Hemlocks also are associated with 19 other forest types (Table 1) throughout their ranges (Fowells 1965). Exhibiting some traits of a pioneer tree species, it is often found with stands of white pine that began after fire, windthrow, or other catastrophic disturbances (Hough and Forbes 1943, Lutz 1930, Maissurow 1935, Miles and Smith 1960, Morey 1936). Hemlocks can colonize established forest stands and slowly become the dominant species without any major disturbances, which makes it a climax species (Graham 1941a, Hough 1936a, Martin 1959).

Life history

When hemlocks mature, they can be extremely large and old with the records at 988 years old, diameter breast height (dbh) of 213.4 cm, and 48.8 m tall (Frothingham 1915, Morey 1936). In Tennessee, the average for a 60-year-old tree is a diameter of 10.4 cm and a height of 9.1 m (Table 2), and the averages for the same age tree in New York (6.4 cm diameter and 6.1 m) or Michigan (9.7 cm diameter and 7.6 m) are slightly lower (Frothingham 1915). Some hemlocks with less than 2.5 cm dbh can be over 100 years old, and 5.1 to 7.6 cm saplings may be up to 200 years old (Fowells 1965). In light to medium shade, vigorous seedlings and saplings may grow 20.3 to 30.5 cm tall per year and can grow 45.7 cm or more with enough soil moisture (Fowells 1965). Hemlocks that have a history of suppression and release may have better final growth than those growing without any suppression (Marshall 1927). Hemlock is tolerant of low light intensities (Bourdeau and Laverick 1958), and older seedlings can live with only 5% of full sunlight (Burns 1923, Grasovsky 1929). Over long time periods (200 to 400 years), hemlocks are more competitive than any other associated tree species (Hough 1936a, Hough and Forbes 1943).

Male and female differentiation of flower buds becomes apparent at the beginning of July in New York and Pennsylvania, and strobili are well formed by the end of July for males and by October for females. From April to early June, flowers appear depending on latitude, seasonal advance or elevation (Frothingham 1915). Following cone maturity, small winged seeds are shed during the fall and winter, and the hygroscopic cone scales

Table 1. Forest types in which eastern hemlocks are associated in Northern and Central forests in North America (Fowells 1965).

Location	Type number	Forest type
Northern forests	5	Balsam Fir
	15	Red Pine
	18	Paper Birch
	20	White Pine - Northern Red Oak - White Ash
	21	White Pine
	25	Sugar Maple - Beech - Yellow Birch
	28	Black Cherry – Sugar Maple
	31	Red Spruce – Sugar Maple - Beech
	32	Red Spruce
	33	Red Spruce – Balsam Fir
	37	Northern White - Cedar
	39	Black Ash – American Elm – Red Maple
	60	Beech – Sugar Maple
Central forests	29	Black Cherry
	34	Red Spruce – Fraser Fir
	77	Shortleaf Pine – Virginia Pine
	97	Atlantic White - Cedar
	54	Northern Red Oak – Basswood – White Ash
	59	Yellow-Poplar – White Oak – Northern Red Oak

Table 2. The average diameter breast height (dbh), height, and age of hemlock trees of all crown classes in Michigan, Tennessee, and New York (Frothingham 1915, Fowells 1965).

	Michigan		New York		Tennessee	
Age (yrs)	dbh (cm)	Height (m)	dbh (cm)	Height (m)	dbh (cm)	Height (m)
40	5.3	4.9	3.6	4.0	4.8	4.9
60	9.7	7.6	6.4	6.1	10.4	9.1
80	14.5	10.7	10.2	8.5	17.0	13.4
100	19.8	13.4	14.0	11.0	23.9	17.7
120	25.4	16.2	18.5	13.7	30.0	21.0
140	31.2	18.3	23.9	16.5	35.6	23.5

open when it is dry but close when conditions are wet. Seed dispersal occurs during dry windy weather, which favors wide dispersal for the seeds (Fowells 1965). Every two to three years, a good seed crop occurs in mature hemlock stands (Frothingham 1915), and the trees begin to fruit from 20 to 40 years old in the open and from 30 to 50 years in areas with moderate light (Merrill and Hawley 1924). Trees that are suppressed under a dense canopy will not fruit regardless of age, and cones will be produced for 450 years or more by mature, dominant, old growth trees (Hough and Forbes 1943).

Only 20% to 30% of hemlock seeds germinate, but development can be increased with seed stratification and suitable temperatures (Baldwin 1930, 1934; Barton 1930). Seed germination occurs in March or April in the southern United States and continues until late June or July in the North. Initial survival and germination of hemlocks are the most successful in shaded, moist and cool sites (Fowells 1965). Germination is influenced by length of day (Olson 1954) and the interaction of photoperiod and temperature (Olson et al. 1959, Stearns and Olson 1958). Moist, well-decomposed litter, rotted wood, mineral soil, and moss mats on soil or rocks are all favorable conditions for seed germination (Eyre and Zillgitt 1953, Goder 1956, Hough 1943).

Seedling development during the first growing season is slow, and the shoots will be 2.5 to 3.3 cm by fall. After the first season, the root system contains a short taproot, which is 2.5 to 13.0 cm with a few laterals, and the taproot will be lost in the successive years as the laterals continue to grow. The early survival of hemlock seedlings is dependent upon the availability of continuous moisture in the upper soil horizon and adequate light throughout the year. Seedlings establish better in shade than full sun because the soil in full sunlight dries out too quickly for the shallow roots (Fowells 1965). Hemlock seedlings will grow well with light as low as 20% of full sunlight and maintain their roots below the level of surface soil drying (Lutz 1928). Full sunlight also causes direct heat injury in the form of lesions on seedling stems (Fowells 1965). Damping-off and root-rot fungi are common for hemlock seedlings in natural seedbeds and in the nursery (Olson 1954). The slowest growing seedlings are often smothered under hardwood leaf fall for three to five years of their life initially in a hardwood forest (Fowells 1965).

Insect diversity on eastern hemlock

An insect biodiversity study in the Great Smoky Mountains National Park yielded 2,832 specimens representing 292 species in 101 families and ten orders from malaise traps in the canopy of eastern hemlocks (Buck et al. 2005). The total number of specimens recorded on eastern hemlocks lies within the same range as other trees like tulip-poplar and red oak (LaForest 2000, Trieff 2002) within the region. Over 94% of the species were from the orders Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Hemiptera. Eastern hemlocks in forest settings contain a species rich and stable insect fauna. Hemlock insect biodiversity is important to the health of forest systems (Buck et al. 2005), and certain insect species rely on the microclimate of eastern hemlocks.

Potential keystone species, such as the snail-feeding carabid *Sphaeroderus stenostomus* Weber, the mycetophilid *Monoclona rufilatera* Walker, the fungal feeding *Dryomyza simplex* Loew, and the hemlock scale, *Abrallaspis ithacae* (Ferris), were widespread and well established on the eastern hemlock (Buck et al. 2005). Two exotic species of Hemiptera were found during this study that could impact hemlocks. The hemlock woolly adelgid (HWA), *Adelges tsugae* Annand, was discovered at eight sites in the Park in 2002, and it has since become a major pest of eastern hemlock throughout the region (Buck et al. 2005). The elongate hemlock scale (EHS), *Fiorinia externa* Ferris, also was found and is capable of co-existing with the HWA (McClure 2002a). The invasion of exotic insect species has severe impacts on the health and the habitat structure of forest systems (Buck et al. 2005).

Abiotic and biotic factors affecting eastern hemlock

Many abiotic and biotic pests of hemlocks occur in hardwood forests (Fowells 1965). Because hemlock is shallow rooted (Frothingham 1915), it is more susceptible to droughts, with severe droughts causing mortality (Hough 1936b, McIntyre and Schnur 1936, Secrest et al. 1941, Stickel 1933). The shallow roots also predispose it to uprooting by the wind (Eyre and Zillgitt 1953, Hough 1943, Stoeckeler and Arbogast 1955), and windthrow often occurs at wet sites and on shallow or slow draining soils that are

waterlogged from heavy rains (Fowells 1965). Injury and some mortality occur when hemlocks are suddenly exposed from logging or windthrow of nearby trees (Eyre and Zillgitt 1953). Factors that lead to mortality for exposed trees are sunscald and damage to feeding roots from higher soil temperatures (Graham 1941b, Graham 1943, Secrest et al. 1941). Young hemlocks are highly susceptible to fire damage. Older hemlocks may survive because of their thick bark, but the roots are often injured by any fire that burns deeper than loose surface litter (Fowells 1965).

Hemlock is host to 24 pest insects, but only three insects are of economic importance (Fowells 1965). *Melanophila fulvoguttata* (Harris), the hemlock borer only attacks weakened trees, but *Lambdina fiscellaria fiscellaria* Hulst and *L. athasaria athasaria* (Walker), two hemlock loopers, can defoliate or cause localized mortality of trees (Walters 1956). Few disease-causing organisms cause death or decay losses in living hemlock, which is rarely infested with red belt fungus (*Fomes pinicola* (Schwartz: Fr.) Karst.), rusty conk (P*olyporus gilvus* (Schwein)), and *P. borealis* (Wahlenb.). Heart rot is caused by red ring rot fungus (*F. pini* (Thore:Fr.) Fr.) (Percival 1933), the velvet top fungus (*P. schweinitzii* (Fr.) Pat.), the brown butt rot (*P. balsameus* Peck), and white root conk (*Poria subacida* (Pk.) Sacc.) (Fowells 1965). Sometimes weakened trees are damaged by honey fungus or shoestring rot (*Armillaria melea* (Vahl.: Fr.) Kumm.) (Secrest et al. 1941).

Exotic pests of eastern hemlock

The natural populations of eastern hemlock have recently begun to decline in much of their range in the eastern United States as a result of the exotic HWA (McClure 1980a, 1991, Souto et al. 1996, Royle and Lathrop 1997, Danoff-Burg and Bird 2002). HWA was first documented in New York State during the 1990s, and it was present at this time in ten other eastern states from North Carolina to Massachusetts (Souto et al. 1996). In Japan, natural enemies maintain populations of HWA below pest status on hemlock trees, but in the United States, populations of HWA reach pest status on eastern

hemlock because of the lack of natural predators, competitors, parasitoids, and minimal chemical host resistance (McClure 1995, 1996, McClure and Cheah 1999). Individual eastern hemlock trees and whole stands declined rapidly after HWA infestation (McClure 1990, 1991). The damage and mortality from HWA in the eastern hemlock forests may differ in a single stand or across large areas consisting of a large range of ages and sizes of trees (Orwig and Foster 1996). Environmental conditions such as elevation, terrain shape, and distance from streams appear to affect population numbers for HWA infestations or cause some stands to be more sensitive to attack (Young et al. 1999). Even though HWA exhibits greater mortality in regions with low minimum temperatures, a small amount of specimens could be cold tolerant (Parker et al. 1998). HWA could invade the remainder of the eastern hemlock range rapidly because of its cold tolerance, ability to disperse by wind, attachment to tree bark or animals for transportation, and survival for several days without feeding (McClure 1987, 1990).

A second introduced Asian insect, EHS, infests stands and weakens trees throughout the range where eastern hemlock is grown (Danoff-Burg and Bird 2002). The scale feeds on the underside of eastern hemlock needles causing plant tissue discoloration and premature needle drop. The survival, development rate, and fecundity of EHS are associated with the nutrient quality of eastern hemlock, which is influenced by scale density and the edaphic conditions of the site (McClure 1980a, 1981a, 1983c). If HWA is previously present, then extended and heavy attacks of EHS would add to tree mortality (Danoff-Burg and Bird 2002).

Considerable decline in the eastern hemlock range will occur unless effective natural enemies of both pest species are found and successfully employed to deter further dispersal (Orwig and Foster 1996). Understanding how both of these exotic insects impact hemlock stands is an essential step towards reducing eastern hemlock mortality (Danoff-Burg and Bird 2002). The environmental factors that determine the spread and establishment of harmful infestations and the spatial distribution of trees infested with EHS and HWA were studied. Every tree sampled had HWA and EHS present in the Black Rock Forest in New York. Sixty-six percent of the eastern hemlock trees sampled had a medium HWA infestation level with 14% of trees that were highly infested. EHS

had more trees (42%) classified as highly infested and 88% of trees lacked new growth and the majority trees had a medium level of needle loss. There were similar mean values for HWA, scale presence, leaf loss, and new growth when evaluated by distance from the stream or between the eastern and western slopes along the sub transects. They found that an increased EHS and HWA infestation levels led to decreased new growth, and an increased EHS infestation also led to higher needle loss and decreased new growth (Danoff-Burg and Bird 2002).

In the Black Rock Forest, both pest species were present in large numbers (Danoff-Burg and Bird 2002). Data from this study indicate that EHS and not HWA could be the main cause of hemlock decline in this forest, which is in contrast to the assumption among foresters in this area (D'Arrigo et al. 2002, Danoff-Burg and Bird 2002). This belief was based on other studies that have reported high amounts of needle loss and tree mortality from only HWA infestations (Orwig and Foster 1996, McClure 1996). HWA may fluctuate widely across forest landscapes and microenvironments (Orwig and Foster 1996), and the relatively fine-scale data supported this inference. In contrast, this study determined the impact of EHS on tree mortality may be equal to that of HWA (Danoff-Burg and Bird 2002). Suppression of new growth on an eastern hemlock happens before needle loss as the tree declines from increasing levels of phloem-feeding pests. They proposed HWA could first weaken trees because of the low level of new growth in highly infested trees, and EHS establishes on the declining trees and undergoes a population explosion causing most of the needle loss and possibly tree mortality. The composition of nutrients in hemlock stands is altered by HWA (Jenkins et al. 1999), and the reduction in tree health allows EHS to invade (Danoff-Burg and Bird 2002).

Elongate hemlock scale was a more effective competitor than another exotic scale, *Nuculaspis tsugae* (Marlatt), on eastern hemlock in the northeast (McClure 1980b), and it also may be more competitive than HWA (Danoff-Burg and Bird 2002). Insects are more effective competitors in the geographic center of their distribution than at the edge of their range because of environmental stresses (Huston 1994). EHS may be a superior competitor because the forest microclimate has less impact on it. It excludes HWA in

large populations, and it feeds until the tree dies. When HWA and EHS occur on the same trees, new strategies for reducing HWA populations and mortality should be evaluated. These findings are most applicable in areas where EHS is more abundant than HWA, due to populations of the latter being cold stressed. Therefore, EHS could be equally important as HWA to consider when formulating control measures to protect eastern hemlock (Danoff-Burg and Bird 2002).

Fiorinia externa Ferris

Background: Exotic scale insects

For introduced exotic species, habitats with suitable climates and appropriate resources can help species experience rapid population growth. Plentiful food along with a lack of indigenous competitors or natural enemies permits their numbers to increase exponentially until the food supply is depleted. Species competition is best studied in areas where the factors regulating the native communities are absent (McClure 1980b). The red pine scale, *Matsucoccus resinosae* Bean and Goodwin, is an example of an exotic phytophagous insect species that quickly exhausted its food supply, which had negative effects on the survival, development rate, and fecundity of the scale (McClure 1976, 1977a). Many species of scale insects have become severe pests around the world (McClure 1980b). A list of exotic scales from DeBach and Rosen (1976) contained 47 scale species from the Diaspididae, for which numerous, expensive biological control projects were initiated (DeBach et al. 1971, DeBach 1974). The use of predators in the families Coccinellidae and Nitidulidae has been demonstrated to successfully reduce pest populations of other scale insects (Kosztarab 1996).

Introduction and spread in the United States

Elongate hemlock scale was introduced into the United States on exotic hemlocks between 1908 and 1910 in a New York City shipment of exotic hemlocks from Japan and became established on native eastern hemlock throughout the region including Long Island, New York (Sasscer 1912). The scale was originally identified as *F. japonica*

Kuwana (Sasscer 1912), but Ferris (1942) described it as a new species based in part on materials collected by H S. McConnell from Baltimore, MD and Queens, NY. The primary hosts of EHS are ***T. canadensis***, *T. caroliniana* (Carolina hemlock), and *T. diversifolia* (Japanese hemlock), and the secondary hosts include yew, spruce, and fir (Garrett and Langford 1969). From records at the United States National Museum, EHS was reported from Ohio in 1929, Connecticut in 1929, Maryland in 1939, Pennsylvania in 1946, New Jersey in 1950, and the District of Columbia in 1952 (Garrett and Langford 1969). Bray (1958) reported it in Massachusetts (Garrett and Langford 1969). EHS infestations on eastern hemlocks in Knox County, TN, were found in 2004 (Buck 2004). In areas of Connecticut and other parts of the northeast, EHS has become a major pest of eastern hemlocks in forested and urban areas with trees weakened or killed by this pest (McClure 1977b). EHS infestations on ornamental plantings were the source of an isolated and heavy scale population in the residential area of New Haven in Connecticut (McClure 1978a).

Life history

Adult female EHS are about 2 mm long, and adult males are about 1.5 mm long (McClure 2002b). Their flexible stylet is about three or four times the length of the body (Wallner 1965, Johnson and Lyon 1976) and allows them to extract fluid from mesophyllic cells (McClure 1980a). The adult female EHS lives within the exuviae of the last molt of the second instar forming a pupillarial test (Ferris 1942). This behavior distinguishes it from most female diaspidids in this genus. After completing its last molt, the female contracts as the eggs are laid and shrinks to occupy only the anterior one-third of the exuviae, and the posterior is filled with eggs that are laid in two rows with their ends meeting in the median longitudinal axis of the test with an average of six eggs developing at one time. Crawlers emerge and escape from the posterior end of the female scale, and chorion counts taken from beneath the coverings of living egg-laying females on the previous year's growth showed an average of 20.4 eggs laid (Davidson and McComb 1958). Eggs hatch in about one month, and crawlers move to new needles on

the same hemlock tree (Wallner 1965, Johnson and Lyon 1976). The crawlers are soft-bodied, lemon-colored and about 0.1 mm long (McClure 2002b).

The crawlers are active after leaving the female scale and settle within 48 hours or so on one of the two white stripes (stomatal bands) that parallel the midrib on the ventral surface of the needle (Davidson and McComb 1958). These stripes are produced by the needle to protect the stomates and continue to develop over the dorsum of the nymphs disrupting the outline of its body (Lambdin et al. 2005). The crawlers insert their stylets into the stomata and remove nutrients from the needle (Lambdin et al. 2005). After a crawler settles, it starts to secrete two types of waxy coverings. The layer with a frosty-appearance is secreted from the posterior end and covers the entire first instar. At the same time, two long waxy threads are secreted from a pair of glands located between the antennae on the anterior margin of the head, and these threads form a mass of tangled and trailing white threads that gives infested trees a mealy appearance (Davidson and McComb 1958). After 3 to 4 weeks, the crawlers molt (Wallner 1965, Johnson and Lyon 1976).

The second instar nymphs are 0.1 to 1.0 mm long (McClure 2002b). EHS females have three developmental stages, while males have five stages with the two additional stages being the prepupa and pupa (Lambdin et al. 2005). After becoming a second instar, male and female EHS lose their legs and eyes and the antennae are reduced to one-segment (Lambdin et al. 2005). Adult females produce a grayish-brown waxy covering or test, and the males produce a white test with parallel sides (Lambdin et al. 2005). The females mature after about one month, and males emerge around this time as small and delicate winged insects (Wallner 1965, Johnson and Lyon 1976). Males complete their prepupal and pupal stages inside the second stage test, and mature males back out of their test through a flap at the posterior end. EHS males do not feed after maturity and live 24 to 72 hours after emergence from the test. Usually males walk across the needles to seek females for mating, even though they are able to fly (Lambdin et al. 2005). About one and a half to two months after mating, the eggs are produced under the test of the female (Wallner 1965, Johnson and Lyon 1976).

From monthly field observations, all developmental stages of males and females along with active crawlers are found throughout the entire year, but the highest reproductive activity occurs during spring and fall in Maryland (Davidson and McComb 1958), Virginia (Kosztarab 1996), and North Carolina and Tennessee (Lambdin et al. 2005). Oviposition is only interrupted by cold weather (Wallner 1965, Johnson and Lyon 1976). EHS has two complete, overlapping generations per year in the southern Appalachians (Lambdin et al. 2005), and the same is true for other Southern and Mid-Atlantic States. Only one generation generally occurs in the Northeast (McClure 2002b). In the southern Appalachians, crawlers peaked in June for spring emergence and in late October into November for the fall emergence (Lambdin et al. 2005). The fall peak emergence of males occurred in August when the greatest numbers of adult females were present, and gravid females were most numerous from late May through October and November (Lambdin et al. 2005). Densities of EHS ranged from 0.2 to 1.6 scales per hemlock needle, and EHS densities ranged from 1.3 to 10.1 scales per needle the next year (McClure 1981b).

Dispersal

Wind is an important method of dispersal for the mobile first instars (Beardsley and Gonzalez 1975, McClure 1977b). Mature females of the California red scale, *Aonidiella aurantii* (Maskell), were dispersed by wind up to 312 m (Willard 1974). The impact of scale dispersal from the original colonization sites showed distribution and abundance patterns for *M. resinosae* in a Connecticut red pine plantation (McClure 1979b). Milder weather in midspring and fall allows a longer developmental period where a partial second generation may occur with crawlers emerging at the end of September and October. Wind during these months could help disperse crawlers to infest new trees (McClure 1977b).

The largest number of crawlers was collected along the Northeast transect from wind dispersal tests when the wind blows from the South and Southwest, and the fewest crawlers were found in the northwest transect (McClure 1977b). Live crawlers were transported from 15 to 105 m by the wind; with most of the crawlers found at 15 m on the

leeward side of the infested tree stand. Different stages of EHS were carried by wind and became trapped on sticky plates for all canopy heights in the forest (McClure 1979b). Male adults were found reasonably evenly and more often than any other stage in the canopy on the plates, but they do not help directly establish new populations. The remaining developmental stages and scale-infested hemlock needles were trapped most often in the lower canopy at 5 m and least in the upper canopy at 15 m. Most of them probably settle in the lower canopy because they are not strong fliers and do not resist gravity. Crawlers were the chief stage for dispersal and were found in the highest numbers. The amount of eggs, adult females, and infested hemlock needles found on the plates were high enough to associate them as important agents for local dispersal (McClure 1979b).

Environmental factors

Seven soil treatments were compared for EHS survival, which represented different soil types where eastern hemlocks grow. A similar number of scales were found on all of the trees with the most living scales and gravid females on fertilized trees and the least number on trees planted in soil containing lime. The new-growth needles in the lower crown were colonized the most frequently. Reduced health of hemlocks from high pH soils, severe root pruning, or hydric and xeric conditions led to a lower survival and development rate of the EHS. Application of fertilizer was found to decrease the stress on the trees allowing better resistance to insects, but over fertilizing can lead to higher numbers of scales because of the high concentrations of nitrogen, phosphorus, potassium and other nutrients (McClure 1977b).

The nitrogen concentration for new foliage on infested hemlocks was lower than for un-infested trees. Fertilizing during the spring increased the foliar nitrogen concentration, which improved nymph survival. This observation confirms the deleterious effect of scale density on food quality and involves nitrogen as a critical nutritional element for the self-regulatory mechanism of EHS populations on hemlock (McClure 1980a). EHS nymphs had greater mortality, slower development, and fewer progeny produced on trees with poor sources of nitrogen in the foliage. The changes in

the amount of nitrogenous food related to physiological stress effected the survival and reproduction of psyllids that fed on *Eucalyptus* (White 1969). Populations of aphids, chinch bugs, and scales also responded positively to improved nutrient quality, especially to increased nitrogen concentration (Rodriquez 1960). On 14 preferred evergreen hosts of EHS, scale populations had 41% less mortality, developed 47% faster, and produced twice the number of eggs per female on species with higher concentrations of nitrogen and water in young needles (McClure 1980a). Water shortage is the most important factor that provides proper conditions for insect outbreaks (Stark 1965, White 1974, McClure 1980a), and moisture stress changes the food quality of a host by impacting nitrogen uptake and metabolism (Mattson and Addy 1975). These data conclude that the presence and number of feeding nymphs had an influence on the quantity and quality of the foliage available for feeding (McClure 1981b). The suitability of EHS to various native and exotic conifers is related to the nutritious quality of the young foliage during peak nymphal development (McClure 1980a).

Competition

Previous evidence has suggested that overpopulation limits EHS numbers and that nutrition has an important role in the mechanism of self-regulation (McClure 1981b). On hemlocks with scale densities that were reduced 50% by insecticide application, the surviving scales and colonists developed more quickly and females had higher fecundity than those on untreated, control trees (McClure 1977c). Survival, development rate, and fecundity decreased with increasing scale density, which indicates that populations of EHS are somewhat self-regulated (McClure 1981b). Drastic reductions in tree growth and in the amount of healthy needle tissue sometimes reduce the nutritive level of the host to a level where the scales die of starvation, but the tree recovers (Wallner 1965, Johnson and Lyon 1976).

Parasitism of elongate hemlock scale by *Encarsia citrina* (Craw)

The effectiveness of parasitoids in regulating host populations depends on their relative spatial distributions and their ability to respond to changes in the host density

(McClure 1977d). Several studies examined the environmental factors that affect distribution of scale insects in a tree crown (Bliss et al. 1935, Schweig and Grunberg 1936, Gentile and Summers 1958, Beardsley and Gonzalez 1975), but few have examined the spatial relationships between a scale insect and its parasitoid (McClure 1977d). Six species of parasitic wasps were reported from EHS, but none were abundant enough to effectively regulate scale populations (Davidson and McComb 1958, Wallner 1964, 1965, Talerico et al. 1967, McClure 1977d). *Encarsia citrina* (Craw) in New York and *Prospaltella* sp. in Maryland (Hymenoptera: Eulophididae) were the two most common parasitoids and accounted for 6.0 to 16.6% parasitism, respectively (Wallner 1964, Davidson and McComb 1958).

In contrast, parasitism levels of second instar females EHS by *E. citrina* at several locations in Fairfield County, CT, in 1976 were often more than 50% and as high as 72%, and it was the only parasitoid collected and observed within second instar females (McClure 1977d). The highest numbers of EHS and *E. citrina* occurred in the lower crown, where 49 and 70% of the total numbers for each were collected, respectively. The upper crown had the lowest numbers with 19% of scales and 6% parasitoids. Parasitism was greatest on trees supporting the highest host densities. The average density of EHS females was 352.5 from 400 needles, and mean parasitism was 42.1% for *E. citrina* in September, which were considerably higher than in May when the mean female density was 312.4 from 400 needles and mean parasitism was 28.5%. *Encarsia citrina* shows a density-dependent response to EHS vertically within the crown and among lower crowns of infested hemlocks. These data indicate the potential value of this parasitoid for biological control (McClure 1977d).

Encarsia citrina was the only parasitoid recovered from EHS and is the first documented case of this species in eastern Tennessee (Lambdin et al. 2005). It had a wide distribution at urban and forest sites in eastern Tennessee and North Carolina, and emergence holes were documented on male (< 1%) and female tests. The percent of emerged parasitoids was 16 to 33% at urban sites and 20 to 22% in forest sites. August was the peak for parasitoid emergence, but emerging parasitoids were found from June through November. Female *E. citrina* oviposit on late first and second instars, and only

one adult wasp will develop fully from each host. During the pupal stage, the parasitoid positions itself on its back, and the adult chews sub-circular holes in the center of the host and emerges by placing its prothoracic legs through the hole, followed by its head and pulls itself out of the host. It flies to a group of scales and then it uses a short hop-like flight pattern along with tapping antennae to search for a host on the needles. The overwintering stage of parasitoid has not yet been concluded (Lambdin et al. 2005).

Fiorinia externa and *Nuculaspis tsugae* in Japan and the United States

Comparison of endemic and exotic scale populations

Endemic insect herbivore populations usually do not reach densities high enough to deplete resources from the host or kill the host plant because of different interacting factors like weather, characteristics of host plant, other herbivores and natural enemies (McClure 1983a, b, 1986a). However, introduced species frequently multiply quickly and may severely injure new host plants (McClure 1983a, b, 1986a). For exotic populations, single mortality factors are evaluated easier, because the communities related to the species are new and uncomplicated with few regulators of population growth as compared to the endemic community (McClure 1981a, 1983b, 1986a). Even though numerous introduced herbivores have resulted in hundreds of biological control projects worldwide during the 1900s (Clausen 1978), few studies address endemic and exotic populations. Studies comparing endemic and exotic populations may offer important information about how factors can be used to control populations of destructive introduced species and help evaluate the performance of natural enemies that have been introduced for biological control (McClure 1986a).

Endemic populations of EHS and *Nuculaspis tsugae* (Marlatt) (Hemiptera: Diaspididae) in Japan were studied, and the results were compared to the introduced populations in the United States (McClure 1986a). Both of these scales were widely distributed in Japan in 13 natural and cultivated stands of *T. diversifolia* Masters and *T. sieboldii* Carriere that were sampled in Honshu, but the scale densities found were

harmless to the trees and considerably lower when compared to densities in North America. Both diaspidids had significantly higher densities, survivorship, and fecundity on eastern hemlocks planted outside their natural range in Japan than on naturally occurring montane trees, and they also were higher on *Tsuga* species not found in Japan than on native Japanese hemlocks. When trees grow outside of their natural habitats, they are more susceptible to damage from insect herbivores because of the stress from poor growing conditions. Fecundity was higher among scales that had been transferred to a tree of the same species than in scales relocated on a different species for all hemlock species tested (McClure 1986a).

Both EHS and *N. tsugae* are originally from Japan (Takahashi and Takagi 1957, Takagi 1963) and are now serious pests of *T. canadensis* from North America (Sasscer 1912, Weiss 1914, Ferris 1936, McClure 1986a). Infested trees can die within 10 years, but chemical control is effective and available for ornamental hemlocks (McClure 1978c, 1980b). Chemical treatments in the forest, however, are unsuccessful with scale populations recovering rapidly (McClure 1977b, 1986a). The most important mortality factors for these exotic scale populations were parasitism by *E. citrina* and nymph competition for food (McClure 1979a, 1980b, 1981a, 1986a), but neither factor slowed the scale populations from rapid growth or stopped damage and decline of the hemlocks (McClure 1986a). Studies from McClure (1983c) showed that the two species of scale had a higher fecundity on the native Japanese hemlocks than on North American *Tsuga* species.

Life history and competition for resources

The physiological status of a host plant is important to the success of populations of phytophagous insects (Southwood 1973, McNeill and Southwood 1978, McClure 1980b). Numerous studies have established the dynamic nature of host nutritional quality for piercing and sucking insects not only during the season (Dixon 1970, 1975, van Emden et al. 1969, Webb 1977, Webb and Moran 1978, White 1978) but also throughout the course of an infestation (McClure 1977a, 1979a, 1980b).

Hatching early in June two to four weeks before its competitor (*N. tsugae*), EHS has a distinct spatial and nutritional advantage by colonizing young needles at a time during the year when foliar nitrogen concentrations and water are high. This reduces the amount of foliar nitrogen available to nymphs of *N. tsugae*, which forces crawlers of *N. tsugae* to colonize older, nitrogen-poor foliage, resulting in greater mortality (McClure 1980b). Foliar nitrogen concentration was reduced more than 18% after 7 weeks of feeding by EHS. For mixed-species infestations, EHS nymphs suffered less mortality than in single-species infestations, even though total scale densities were higher in mixed infestations. Nymphs of *N. tsugae* suffered more mortality in mixed-species infestations, even though total scale densities were lower than in *N. tsugae* single-species infestations. For all infestations, percent mortality after five weeks was significantly higher among colonists feeding on the older needles than among those feeding on younger ones. For six trees infested only with EHS, percent survival and fecundity over two years were highest on trees that supported the lowest scale densities, and percent survival was lowest on the most heavily infested tree. By the end of the study, sites with small populations of *N. tsugae* were eliminated by *F. externa*. At two sites where *N. tsugae* was abundant and *F. externa* was scarce, *N. tsugae* was able to maintain its initial population (McClure 1980b).

Parasitism

Scale populations on ornamental trees in Japan have the potential to reach densities high enough to cause damage to a tree, but it rarely happens because the parasitoids *E. citrina* and *Arrhenophagus albitibiae* Girault typically kill 90.2 to 94.2% of both scale species (McClure 1986a). In Honshu, high parasitism did not cause much change in endemic scale populations because of the susceptible stages of EHS and *N. tsugae* available for parasitsim. For the two scale species in Japan, parasitism was a main factor in keeping the scale populations from increasing rapidly. The populations of EHS are higher in Connecticut on *T. canadensis* than on Japanese trees because the *E. citrina* populations are asynchronous with the univoltine scale host (McClure 1986a).

Encarsia citrina is a primary internal parasitoid for both scale species, and it exhibited a density dependent response to both scales in single-species infestations. In mixed infestations, it did not attack the more abundant species but attacked each scale in proportion to the total scale numbers. It did not alter the outcome of the competition between the summer generations of the two scales (McClure 1980b). *Encarsia citrina* has 50% parasitism common in southwestern Connecticut with some areas as high as 96% (McClure 1978b, 1980b). The seasonal abundance of ovipositing adults of *E. citrina* was closely synchronized with the first-instar nymphs of *N. tsugae*, which were a suitable stage for parasitism (McClure 1978b). Both the parasitoid and scale were bivoltine and had similar rates of development. A permanent parasitoid-host relationship could be preserved in areas where EHS and *N. tsugae* occur together, and the adult parasitoids emerging from one host species would readily attack the other (McClure 1978b, 1980b).

Chemical control of elongate hemlock scale

Control of EHS has been successful on ornamental hemlocks using chemical insecticides (McClure 1977c, 1978c). Armored scales usually are controlled with insecticides applied during the crawler stage that are vulnerable because they lack a fully developed test. Chemical control was synchronized with peak abundance of crawlers, which occurred when adults of predators and parasitoids of the first generation were most abundant (McClure 1979b). Studies indicate that effective control of scale insects may be achieved using insecticides to kill adult males and females and by using sex attractants to disrupt mating (Miller and Kosztarab 1979, McClure 1979b). The control of EHS in our eastern forests may depend on the successful manipulation of pesticides, natural enemies, pheromones, and host quality in an integrated system of pest management (McClure 1979b).

Resurgence of insect populations after insecticide application has been well documented (Ripper 1956, Price 1975). Post-spray populations of phytophagous insects often rebound quickly as the result of reduced numbers of natural enemies, reduced

competition among individuals, and increased plant growth which improves the nutritive quality of the host (McClure 1977c). Sixteen coccid species had population outbreaks following pesticide application (Ripper 1956). Outbreaks were attributed to the deleterious effects of pesticides on parasitoids of scales (Lord 1947, Bartlett and Ewart 1951, Bartlett and Ortega 1952). A disproportionate reduction in the density of natural enemies relative to that of EHS following insecticide treatment could also contribute to a resurgence of populations of the scale (McClure 1977c). The improved vigor of citrus trees after treatments of zinc and copper led to greater numbers of the purple scale, *Lepidosaphes beckii* (Newman), and the Florida red scale, *Chrysomphalus aonidum* (L.) (Thompson 1939). Excellent control of EHS was achieved by applying a foliage-drench application of dimethoate insecticide to the entire crown of infested hemlocks (McComb and Davidson 1960, Wallner 1962, Garrett and Langford 1969, McClure 1977c), but this insecticide is currently under review.

The density of EHS 21 days following insecticide application and after the peak of crawlers on completely-sprayed hemlocks was reduced by more than 32-fold, while their density on unsprayed trees increased only 4-fold. The number of dead EHS per 2,000 scales examined from the new needles of each treatment was 1,986 (99.3% mortality) on completely sprayed trees, 1,560 (78.0%) for the sprayed portion of half-sprayed trees, and 64 (3.2%) for the unsprayed portion of half-sprayed trees, and 35 (1.8%) for unsprayed trees. The only parasitoid collected from all trees was *E. citrina*, and few or no parasitoids emerged from either portion of the half-sprayed trees, with percent parasitism on sprayed trees reduced to less than 2% (McClure 1977c). The densities of most predators also were greatly reduced by insecticide application, but there was no reduction observed in the numbers of *Conwentzia pineticola* after dimethoate treatment. The possibility of incomplete pesticide coverage in the forest is high, and results in a high chance for EHS populations to rebound after an application. The natural enemies of EHS should be evaluated to determine the best control methods in the hemlock forests (McClure 1977c).

Predators of elongate hemlock scale

Introduction

Several species of predators occur on EHS-infested eastern hemlock. Common natural enemies of EHS in the northeastern United States are the mirids, *Atractotomus magnicornis* nr. *buenoi* Knight and *Phytocorus* sp., the coniopterygid, *Conwentzia pineticola* Enderlein, and the coccinellid, *Chilocorus stigma* (Say) (McClure 1977c, 1978a). Moderate numbers of *C. stigma* in New York did not cause a noticeable reduction in EHS numbers (Wallner 1965). Numerous spiders also were collected but in low numbers. The predominant insect predators collected by beating infested hemlock foliage during 1976 and 1977 were *A. magnicornis* and *C. stigma* (McClure 1979b).

Adults and nymphs of *A. magnicornis* and adult *C. stigma* were uniformly distributed among 30 forest hemlocks for both sampling dates in 1976 (McClure 1979b), and these predators did not respond numerically to host density. Adults of *A. magnicornis* were trapped on sticky plates in higher numbers in the lower canopy, while those of *C. stigma* were more abundant in the middle and upper canopy. If numbers of adult predators caught on sticky plates are indicative of the vertical utilization of the crown, then the estimates of the importance of *C. stigma* as a hemlock scale predator based upon beating samples taken from the lower crown are conservative. Adults and nymphs of *A. magnicornis* were most abundant on hemlock foliage in June, occurring rarely during mid and late summer, and this pattern of seasonal abundance suggests a single generation each year. Nearly all of the adult mirid bugs were collected during May and June, and adult lady beetles also were most abundant at that time and during September and October (McClure 1979b).

Many generalist and specialist predators are found consuming insect prey on eastern hemlocks in the eastern United States. The following six predators described have been found on eastern hemlocks previously or were found in the initial collection for this study. These predators could be consuming EHS or other Hemiptera species found on eastern hemlocks. Predators such as *C. stigma* and *C. pineticola* were found on EHS infested hemlocks previously, but the control benefits of these insects were not explored.

***Chilocorus stigma* (Say)**

Taxonomic description and distribution

This species was first described by Say (1835) as *Coccinella stigma*. Melsheimer (1853) subsequently transferred it to the genus *Chilocorus* (Gordon 1985). *Chilocorus stigma* is convex, 3.8 to 5.0 mm long and 3.0 to 4.3 wide, and has an oval body shape that tapers posteriorly. This species is black except for one red or yellow spot on each elytron, and it has a smooth dorsal surface (Gordon 1985). The dorsal midline of the thoracic and abdominal regions and most of the dorsum of the first abdominal region segment for second through fourth instar larvae are light cream to white (Muma 1955). First instar larvae are dark gray and approximately one mm long. Second instar larvae are 2.5 to 3.5 mm long, third instar larvae are 4.0 to 5.0 mm long, and the fourth instar larvae are 6.0 mm or longer. Pupal mortality was 18 to 29%, and some reasons for mortality were a predaceous bug in the *Podisus* genus and pupae exposed to the elements (Mayer and Allen 1983). It occurs from the Atlantic coast to the Rocky Mountains in Alberta and the Sierra Nevada but not west of these two mountain ranges in the United States (Gordon 1985).

Biology and life cycle

This species is holometabolous, and the larvae and adults consume the same prey. Adults of *C. stigma* were most abundant during June and October in the northeast, which also suggests a single generation each year with overwintering adults (McClure 1979b). Previous studies have reported two generations per year for *C. stigma* on pine needle scale, *Phenacaspis pinifoliae* (Fitch), in New York (DeBoo and Weidhaas 1976) and three generations per year on *Chrysomphalus aonidum* (L.), in Florida (Muma 1955). In New York, this species overwintered in the duff underneath the trees as an adult and appeared on the first warm day (13° C) in March. Oviposition was first observed in New York in late April. Adults immediately dispersed after eclosion, and they moved from an area with small numbers of prey to areas with higher prey density to prevent competition for a small amount of prey (Mayer and Allen 1983).

Behavior

Adult *C. stigma* do not readily establish themselves on lightly infested trees. Heavy infestations of *Cryptococcus fagisuga* Lindinger, beech scale, were usually associated with a higher predator density than the medium infestations, which in turn supported more predators than did the light infestation. *Chilocorus stigma* moved from tree to tree in search of prey, which it located by tactile or visual cues. Beetles spent half of the time resting, and randomly searched and consumed prey along with other activities during the remaining time (Mayer and Allen 1983). Adult beetles and all four larval stages fed avidly on adult scales (Muma 1955), and this predator was recorded to feed on 18 scale species, seven aphid species, and one coccinellid species (Thompson and Simmonds 1965). The beetles fed only while the maxillary palpi were in contact with the prey, and it pierced the prey with its mandibles and withdrew the body fluids (Mayer and Allen 1983).

Natural and classical biological control

Natural control was observed for populations of pine needle scale, *Phenacaspis pinifoliae* (Fitch), in a monoculture of Scotch pine, and most coccinellids associated with this pest specialize on the family Diaspididae (Deboo and Weidhaas 1976). The use of *C. stigma* as a biological control agent was attempted in many places including Mauritius (Williams 1971), San Diego in the United States (Rosen and DeBach 1978), Uganda (Greathead and Pope 1977), Australia (Wilson 1960), and Bermuda (Bennett and Hughes 1959, Cock 1985). It failed to establish in any of these areas because of other site factors and not climate (Samways et al. 1999).

Harmonia axyridis (Pallas)

Taxonomic description and distribution

This coccinellid was initially described as *Coccinella axyridis* Pallas in 1773, and eight junior synonyms were subsequently proposed for this species (Sasaji 1971, Chapin 1965). The genus was changed three times before *Harmonia* was elevated to generic

status (Sasaji 1971, Chapin 1965), and many subspecies have been described for this species (Korschefsky 1932). This species is also called the Halloween beetle because of its large fall migrations around Halloween (Mahr 1996).

Adult *H. axyridis* are 4.9 to 8.2 mm long and 4.0 to 6.6 mm wide (Kuznetsov 1997), and the body is a moderately convex and shortened oval that is about four-fifth wide as long (Kuznetsov 1997, Sasaji 1971). The head of this lady beetle can be yellow, black, or black with yellow markings, and the pronotum is yellowish with black markings in the center that vary in shape (Chapin and Brou 1991). The lateral edges of the pronotum have a yellow and oval-shaped spot (Chapin and Brou 1991). Elytra for this species have various color morphs that include yellow-orange to red with zero to 19 black spots or black with red spots (Korschefsky 1932). Color polymorphism in *H. axyridis* appears hereditary and is likely associated with a series of multiple alleles (Honek 1996). A transverse plica is present above the apex of the elytra (Chapin 1965, Chapin and Brou 1991). Eggs are oval shaped, 1.2 mm long, and pale to darker yellow (El-Sebaey and El-Gantiry 1999). Larvae are 1.9 to 2.1 mm during the first instar (dark black) and 7.5 to 10.7 mm for the fourth instar, which has orange coloration on the dorsal and dorsal lateral areas of the first abdominal segment and dorsal lateral areas of the second to fifth abdominal segments (Sasaji 1977). Pupae are exposed with the fourth instar exuvium attached to the posterior end of the pupa, and the pupa is attached to a substrate (Savoiskaya and Klausnitzer 1973).

The native range of the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas), in Asia is from the Altai Mountains in the west to the Pacific coast and from southern Siberia in the north to southern China (Korschefsky 1932, Dobzhansky 1933, Chapin 1965, Sasaji 1971, Kuznetsov 1997). *Harmonia axyridis* was first introduced into the North America in 1916 as a classical biological control agent (Gordon 1985), and the first established population was documented in 1988 (Chapin and Brou 1991). Currently, it occurs throughout most of the continental United States except for Montana, Wyoming, and areas in the southwest (Koch 2003).

Biology and life cycle

This species has a holometabolous life cycle with four larval instars (Hodek 1973). Development from egg to adult requires 267.3 degree-days above a lower developmental threshold of 11.2° C in the United States (LaMana and Miller 1998). Temperature influences the rate of development and adult weight, and larvae reared at higher temperatures produce smaller adults than those reared at lower temperatures (Kawauchi 1979). Adults usually live 30 to 90 days depending on the temperature (El-Sebaey and El-Gantiry 1999, He et al. 1994, Soares et al. 2001), but they may live up to three years (Savoiskaya 1970a, b). In the laboratory, females produced up to 3,819 eggs with 25.1 eggs per day (Hukusima and Kamei 1970), and females will oviposit 20 to 30 eggs in a batch (Takahashi 1987).

In the United States, *H. axyridis* is bivoltine (Koch and Hutchison 2003, LaMana and Miller 1996), but four to five generations have been observed for this species (Wang 1986, Katsoyannos et al. 1997). Adults move to overwintering sites during late October in the United States (Kidd et al. 1995, LaMana and Miller 1996), and they land on white or light-colored objects (Obata 1986, Tanagishi 1976). At an overwintering site, they form mass aggregations (Liu and Qin 1989, Tanagishi 1976) in dark and concealed locations (Sakurai et al. 1993). The majority of winter is passed in a state of diapause that is regulated by the corpus allatum (Sakurai et al. 1992). Adults mate and disperse from overwintering sites with warm spring temperatures (LaMana and Miller 1996).

Behavior

Cannibalism plays an important role in the population dynamics of *H. axyridis* (Osawa 1993), and the rate of cannibalism is inversely related to the density of aphids (Burgio et al. 2002, Hironori and Katsuhiro 1997). The intensity of egg cannibalism was density independent for eggs of siblings (Osawa 1993) and density dependent for non-sibling eggs with most intense cannibalism near aphid colonies (Osawa 1989). The cannibalism of larvae increases with the density for larvae of the same species (Michaud 2003).

The peak arrival and oviposition of *H. axyridis* occurs before or at the peak in aphid populations (Hironori and Katsuhiro 1997, Osawa 2000). *Harmonia axyridis* is a predator of many different aphid species (Hodek 1996), and the 90 to 370 aphids are consumed over the larval stages (Hukusima and Kamei 1970). The mean daily aphid consumption by adults was 15 to 65 aphids per day (Hu et al. 1989, Hukusima and Kamei 1970, Lou 1987, Lucas et al. 1997). This species also will feed on Tetranichidae (Lucas et al. 1997), Psyllidae (Michaud 2001, 2002), Coccoidea (McClure 1986b, Yasumatsu and Watanabe 1964), immature stages of Chrysomelidae (Yasumatsu and Watanabe 1964), Curculionidae (Kalaskar and Evans 2001, Stuart et al. 2002), and Lepidoptera (Koch et al. 2003, Shu and Yu 1985).

Natural and classical biological control

Harmonia axyridis has been released many times for classical biological control, and it was released in California, Washington, Nova Scotia, Connecticut, Georgia, Louisiana, Maryland, Washington D. C., Delaware, Maine, Mississippi, Ohio, Pennsylvania, and North Carolina (Gordon 1985). This species was the biological control agent for scales on red pines (McClure 1987) and for aphids on pecans (Tedders and Schaefer 1994). It also has provided control of pests in other systems such as apple orchards (Brown and Miller 1998), sweet corn (Musser and Shelton 2003), and soybeans (Koch 2003). The low densities of this predator the field would not be able to decrease populations of *A. tsugae* on hemlock trees (Wallace and Hain 2000). Mass releases of this lady beetle controlled scale insects in pine forests (Wang 1986).

Rhyzobius lophanthae (Blaisdell)

Taxonomic description and distribution

Rhyzobius lophanthae adults are 1.7 to 2.9 mm long and 1.4 to 2.0 mm wide with an elongate and oval form that is yellowish brown. The pronotum is light reddish brown and, the elytron is dark reddish brown with a faint, green metallic tint (Gordon 1985). *Rhyzobius lophanthae* is native to Australia and an important armored scale predator (Hodek 1973, Rosen 1990, Stathas 2000a). It is found in the southern United States from

California to Florida and north to Maryland along with Arkansas, Tennessee, southern Kentucky, and West Virginia (Gordon 1985). This natural enemy was not introduced into Greece, but it was found in Peloponnese, central Greece, and northern Greece on armored scale-infested olive trees in 1960 (Argyriou and Katsoyannos 1977, Stathas 2000a).

Biology and life cycle

The biological characteristics that make *R. lophanthae* an important predator of different armored scales are prey specificity, fecundity, and adult longevity (Katsoyannos 1996, Rubstov 1952, Smirnoff 1950, Stathas 2000b). It also has good mobility, no parasitism or diapause, and five to seven generations per year (Katsoyannos 1996, Rubstov 1952, Smirnoff 1950, Stathas 2000b). Prey consumption and fecundity help determine the effectiveness of a predator as a biological control agent (Hodek 1973, Stathas 2000b). The rapid population development of *R. lophanthae* (one generation per month during the warm period of the year) makes it an effective biological control agent against diaspidids (Hodek, 1973, Rosen 1990).

For the temperature range of 20 to 25° C and relative humidity from 60 to 80%, *R. lophanthae* lived 27 to 30 days with an average egg development of 6 days, first and second instar larvae at 9 days, third and fourth instar larvae from 5 to 6 days, and pupal development from 7 to 8 days (Smirnoff 1950). Larvae were tested at 25° C for consumption with an average of 1.2 prey eaten for first instar, 2.7 for second instar, 7.5 for third instar, and 24.6 for fourth instar. From the first larval instar to adulthood, the number of scales eaten over a lifetime was 426.6 female scales for males and 708.3 female scales for females. Daily prey consumption was an average of 7 scales for males and 12 for females (Stathas 2000b). Adult longevity decreased as the temperature increased (Stathas 2000a). *Rhyzobius lophanthae* in cages outside at Kifissia, Athens had six generations per year with adult longevity from four to nine months, and the degree-days ranged from 513.9 and 571.2 for the time between each generation (Stathas 2000a).

Rhyzobius lophanthae had an average of 633.7 eggs per female and a daily fecundity between 18 and 25 eggs. Average female fecundity was 633.7 eggs per female and 63.4 days for longevity (Stathas 2000a, b). Females laid a majority (98.3%) of eggs

under tests, and the eggs were found in groups of two, three, four, or five. Some eggs were oviposited singly on the upper surface of the scale test, on potato sprouts, or on the surface of the cage (Stathas 2000b). During the winter months, there were less matings because of the decrease in temperature (Stathas 2000a).

Natural and classical biological control

Rhyzobius lophanthae is a natural enemy of diaspidid scales (Hodek 1973), and it has been recommended in Integrated Pest Management programs for release as an effective predator of scales (Katsoyannos 1996, Stathas 2000b). It has been a successful classical biological control agent in California (Yus 1973), Italy (Bouvier 1913, Smirnoff 1950), Argentina (Salvadores 1913), Bermuda (Bennett and Hughes 1959), Algeria, Tunisia, Morocco (Rungs 1950, Smirnoff 1950), and Georgia (Rubstov 1952) along with spreading naturally to other neighboring countries like Greece (Argyriou and Katsoyannos 1977, Katsoyannos 1996, Stathas 2000b). It was introduced from Australia and released in California to control black scale in 1892, and it also was introduced from South Africa into Texas in 1959. It has been highly successful against a variety of scales in California and other states (Gordon 1985), and this species is available in limited quantities from commercial insectaries (Olkowski et al. 1992).

***Scymnillus* (*Zilus*) *horni* Gordon**

Taxonomic description and distribution

Scymnillus horni Gordon was described in 1985 and is often confused with *Scymnillus arterrimus* Horn, which is native to the western United States (Gordon 1985). The male is 1.4 mm long and 1.0 mm wide, has an oval form, and is black except for yellowish brown mouthparts, antennae, and legs. The head of this species is coarsely punctured, with the punctures separated by a less than one diameter. Its pronotum has lateral coarse punctures, which are separated by one diameter or less, and the discal area is finely punctured with the punctures separated by one to two times a diameter. The elytron is finely punctured as on the pronotal disc with the punctures separated by one to three times a diameter. Its ventral surface is smooth, finely punctured medially, becomes

dull with alutaceous sculpture, and coarse punctures laterally. The female is similar to the male but is 1.5 mm long and 1.1 wide (Gordon 1985).

Scymnillus horni is distributed in the eastern United States on the east coast of Florida, Georgia, and South Carolina and the eastern and central parts of North Carolina. It also is found throughout West Virginia, Virginia, Ohio, Indiana and northern Kentucky (Gordon 1985). Isolated populations of this species also are found in Louisiana at Caddo Parish, East Baton Rouge Parish, and Rapides Parish (Gordon 1985).

Scymnus loweii Mulsant

Taxonomic description and distribution

Scymnus loweii was described in 1850 by Mulsant, and it is distributed throughout the entire continental United States and is found more often in the southwestern United States. The dorsal color pattern is light reddish yellow with a dark median area that extends from the basal portion of the pronotum posteriorly along the elytral suture, and it narrows at the apex of the elytron (Gordon 1985).

Behavior

Scymnus loweii adults and larvae feed on aphids, and 28% of larvae fed on aphids during their initial encounter. This species was not documented to feed on diaspidids. Adults did palpate aphid mummies, but it devoted little time to them after an encounter. The larvae did not feed on aphid mummies during any encounters. When it encountered unparasitized aphids, the larvae grasped the prey by a leg, and it fed by sucking fluids from the prey. It spent a mean of 4,608 seconds feeding on individual aphids, and all aphids were shriveled but intact after the predator terminated feeding. The consumption efficiency of this predator is affected by the ability of the predator to manipulate and orient prey. It is compatible with aphid parasitoid populations after parasitoids have mummified their hosts (Wells et al. 2001). *Scymnus loweii* moved from grain sorghum into cotton fields and was responsible for the pattern of predator movement between the crops (Prasifka et al. 2004).

***Conwentzia pineticola* Enderlein**

Taxonomic description and distribution

Adults in the genus *Conwentzia* can be separated from *Coniopteryx* by the reduced pair of hind wings (Collyer 1951), and the larvae of the genus *Conwentzia* are separated by the pair of fine setae that project over the tarsal claws versus ending bluntly in *Coniopteryx* (Withycombe 1923). *Conwentzia pineticola* was described as a separate species by Enderlein based on only adult characters (Enderlein 1905, 1907). For the wing venation, *C. pineticola* showed variation for the location of the crossvein that joins the stem Rs with connection before the fork-point, point of junction at the fork-point, or beyond the fork-point (Collyer 1951).

Conwentzia pineticola was found at low elevations in the Great Smoky Mountains National Park during 1999 to 2000 as part of the All Taxa Biodiversity Inventory of the park (Stange 2000). This species is found on coniferous trees or orchards in temperate forests of Europe, North America, and Asia (Stelzl and Devetak 1999). In Essex, England it was found on apple, pear, plum, damson, cherry, walnut, and occasionally hedgerow plants (Collyer 1951). This species also was found in Finland orchards (Listo, et al. 1939).

Biology and life cycle

The egg is elongate-oval and is about 0.4 mm long and 0.2 mm wide, and it has a micropylar projection at the anterior pole. Eggs of this species are salmon-pink and darken as the larva develops inside. After a female has laid an egg singly on leaves or bark of fruit trees, it deposits a white, mealy layer over the egg. A newly hatched larva is transparent, without color except for red eyes, and 0.8 mm long. The larva molts twice before becoming a fully-grown third-instar larva (3.4 mm long) with a small head that is partially retracted into the prothorax. The antennae and palpi are translucent with the distal segment of each palp containing fine white hairs. For *C. pineticola*, the body is white laterally with a pair of white areas on each dorsal segment, and the rest of the dorsal area is red. The larva spins a white, circular cocoon that is 4 mm in diameter and rests inside it as a prepupa. Each cocoon has an inner and outer envelope. During the

summer, it is spun on the leaf surface or on twigs, and it is found on or under the bark of tree trunks in autumn (Collyer 1951).

Adults emerge from the overwintering cocoons during April in England, but they emerge earlier when kept at higher temperatures indoors. Adults were present from April through November with two overlapping generations each year. Eggs are laid from April to June after females emerge, and eggs of the second generation are laid in July and August. The second generation of females produce eggs at the end of July, and these eggs will hatch and become adults within three weeks. Males lived more than four weeks, and females lived up to eight weeks. Females laid up to 107 eggs under laboratory conditions (Collyer 1951).

Behavior

Conwentzia pineticola is partially gregarious, and it will be present in large numbers or completely absent. The adults and larvae of this species consume mites (Listo et al.) including *Metatetranychus ulmi* (Koch), the fruit tree red spider mite (Collyer 1951). Larvae will cannibalize each other when food is scarce in captivity, and they were observed consuming eggs of their own species in the field. Larvae pierce the mites and their eggs with their jaws and suck out the contents, and adult *C. pineticola* lift the mites in their jaws and consume them. While searching for food, they move quickly and randomly over a leaf and feel the surface with their palpi. Larvae and adults prefer adult female mites but will consume all stages. The larvae of this species will consume 15 to 35 mites per day, and adults can consume 30 to 40 mites daily (Collyer 1951).

Research objectives

Fiorinia externa is a pest of eastern hemlocks that can weaken or kill these trees that provide a unique habitat for wildlife and promote tourism in the southeastern United States. This pest multiplies quickly and is often undetected because of its cryptic behavior and size. Chemical control is often effective for EHS-infested ornamental planting, but this method is not effective for large hemlock stands. Other control methods using natural

enemies such as predators should be examined as a possible alternative to insecticides. Many predators live on eastern hemlocks and established predators were found on EHS-infested hemlocks in the northeastern United States, but predators of EHS in the southern Appalachians have not until now been evaluated. The objectives of this study were to identify and assess predators of EHS on eastern hemlocks in urban and forest areas in western North Carolina and eastern Tennessee and to evaluate their development, survivability, consumption, intraguild competition, and feeding behavior on EHS.

II. Established predators and their impact on the elongate hemlock scale on eastern hemlocks in forest and urban sites in the southern Appalachians

Introduction

When exotic species invade habitats with suitable climates and appropriate resources, along with the lack of indigenous competitors or natural enemies, species have rapid population growth permitting their numbers to increase almost exponentially until the food supply is depleted. Many species of scale insects have become major pests around the world (McClure 1980b). A list of exotic scales from DeBach and Rosen (1976) contained 47 scale species from the Diaspididae (McClure 1980b), for which numerous, expensive biological control projects were initiated (DeBach et al. 1971, DeBach 1974, McClure 1980b).

Since its discovery during 1910 in New York City (Sasscer 1912), *Fiorinia externa* Ferris, the elongate hemlock scale (EHS), is now established in 14 states throughout the eastern United States, Canada, Asia, and Europe (Lambdin et al. 2005). Upon hatching, mobile crawlers seek a site to settle on the underside of hemlock needles, insert their mouthparts into the needle, and extract fluid from the mesophyllic cells (McClure 1980a). Their feeding results in needles becoming discolored and dropping prematurely, limb-dieback and occasionally tree mortality after extended infestation by EHS **(**McClure 1980a). EHS has become a major pest of *Tsuga canadensis* (L.) Carriere, eastern hemlocks, in the northeastern United States weakening or killing trees in forested areas and ornamental plantings (McClure 1977b).

Eastern hemlock is a late successional tree that provides a unique and more constant habitat than other areas of the forest (Finzi et al 1998, Fuller 1998, Orwig and Foster 1998, Danoff-Burg and Bird 2002). The microclimate is attractive to several species of birds, plants, and fish (McClure et al. 2001, Mitchell 1999, Danoff- Burg and Bird 2002). These trees also are important to tourism in state and national parks because of the aesthetic qualities generated by their presence (Royle and Lathrop 1997, Danoff-

Burg and Bird 2002). The possible extensive mortality of eastern hemlock would have considerable ecological and socioeconomic impact (Royle and Lathrop 1997, Danoff-Burg and Bird 2002).

The control of EHS in eastern forests may depend on the successful manipulation of pesticides, natural enemies, pheromones, and host quality in an integrated system of pest management (McClure 1979b). The possibility of incomplete pesticide coverage in the forest is high, so there is a high probability for EHS populations to rebound after an application. McClure (1977c) noted almost three decades ago that the natural enemies of EHS should be evaluated to determine the best control methods in the hemlock forests.

Natural enemy populations have the unique ability to interact with their prey or host populations and regulate them at lower levels. Several species of natural enemies will only control pest populations at high levels. Some pest species have well over 100 enemies recorded (DeBach 1974). A variety of predators and parasitoids have been used in biological control programs to control pests (Hoy 1994). The coccinellid, *Novius cruentatus* Mulsant, and the parasitoid, *Cryptochetum jorgepastori* Cadahia (Diptera: Cryptochetidae), were introduced as biological control agents of *Palaeococcus fuscipennis* (Burmeister) (Homoptera: Margarodidae), which is an invasive pest of pine in Israel (Mendel et al. 1998). Results from this study showed that the coccinellid was more effective than the parasitoid at high prey densities, but as the scale population decreases, the parasitoid may be a more important regulator of the pest (Mendel et al. 1998). The combination of a predator and parasitoid increased the overall control of aphids on roses (Snyder et al. 2004).

Some predators attack a variety of prey, while other species are more specific. The most commonly recognized predatory insects in pest management programs are found in the orders of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Neuroptera. Over half of all the insect predators are beetles, and species in the family Coccinellidae are often used as biological control agents (Hoy 1994). Predators in the families Coccinellidae and Nitidulidae have been demonstrated to successfully reduce pest populations of other scale insects (Kosztarab 1996). The genera *Axion*, *Chilocorus*, *Coccidophilus*, *Exochomus*, *Hyperaspis*, *Microweisea*, *Rhizobius*, *Scymnus*, *Zagloba*, and

Zilus contain species that feed on armored scales (Diaspididae), with *Chilocorus* consuming the most diverse array of species (Drea and Gordon 1990, Miller and Davidson 2005). *Chilocorus kuwanae* Silvestri was introduced to control *Unaspis euonymi* (Comstock), euonymus scale, in North America (Miller and Davidson 2005), and it was successful in controlling localized infestations from Pennsylvania to North Carolina (Drea and Hendrickson 1988, Nalepa 1992) along with Tennessee (Lambdin 1995) and New Jersey (Matadha et al. 2003). The objectives of this study were to identify and assess EHS predators on eastern hemlocks in western North Carolina and eastern Tennessee.

Materials and methods

Sampling sites

Eastern hemlock infested with EHS were sampled at four sites (two forest and two urban sites). One urban site was located at Lynnhurst Cemetery (Knoxville, TN) (N36°01.268' W083°55.797' elevation 290.78 m) and contained 365 eastern hemlock trees. One urban and one forest site were located at Biltmore Estate (Asheville, NC) (N35°45'00.334" W82°33'00.669" elevation 555.50 m and N35°32'22.481" W82°32'53.142" elevation 680.50 m, respectively), and one forest site was located at Bays Mountain Park (Kingsport, TN) (N36°30.555" W82°36.585" elevation 584.00 m). Sites were sampled from 15 September 2004 to 29 May 2006, except the Bays Mountain Park site that was sampled only from 8 August 2005 to 20 May 2006. Forest sites were defined as dense and unmanaged eastern hemlock-dominated stands or mixed tree stands with plants in the understory, and urban sites as highly managed areas with ornamental plantings of eastern hemlocks and other trees surrounded by roads, parking lots or buildings. Each urban or forest site was arranged into five blocks with 50 trees per block; samples were taken randomly within each block. An EHS infestation ratio from zero to four was taken for each of the 50 trees per block at all sites. The ratings were obtained from counting 12 branches on each tree from the base of the tree to the apex of the tree,

and examining each branch for the presence of EHS. The ratings for infestation were as follows: 1 to 3 infested branches equaled a rating of 1, 4 to 6 infested branches received a rating of 2, 7 to 10 infested branches received a rating of 3, and 11 or more infested branches received a rating of 4. The diameter breast height (dbh) of 10 random trees in each block was taken for all sites.

Site descriptions

Bays Mountain Park is located on top of a ridge with a reservoir lake (0.2 km^2) in the center of the site (13.4 km^2). All five blocks except one were located along the lake. From observations while sampling, the heaviest EHS infestation at Bays Mountain Park is located behind the Nature Center in block three. The other blocks are located to the east or west of block three along the lake. Blocks one and two are predominantly eastern hemlock, but blocks three, four, and five have a mixed forest composition with mature and undergrowth eastern hemlocks found among pine, oak, maple, and poplar trees. Each block, except block one began at the lake and continued back to a trail.

In the early 1900s, this area was indiscriminately logged, and it was logged again from 1915 to 1917 to remove trees and buildings from the area that would be covered by the lake and dam. The Eastman Chemical Company selectively cut mainly oak trees from 1946 to 1948 to produce wood alcohol. In 1944, the use of Bays Mountain Lake for Kingsport's water supply ceased, and the park was officially opened to the public in 1971. No eastern hemlocks have ever been planted at this site, and many of these trees are at least 100 years old. Ken Childress, a Naturalist at the park, first identified the EHS infestation in April 2005 behind the Nature Center, on Lake Road, and near the fire tower.

Lynnhurst Cemetery is located in north Knoxville with a wetland and ridge at the south edge of the property, an apartment complex to the west, a residential neighborhood to the north, and North Broadway to the east. This cemetery (0.53 km^2) has red maple, box elder, cedar, Chinese chestnut, or pine trees lining the roads and surrounding the eastern hemlocks in each block. The main street (Adair Drive) divides the cemetery in half with blocks one and two located on the south side and blocks three, four, and five on

the north side. The small roads within the cemetery divide each half into different blocks, and gravestones are in rows with the hemlocks planted in rows between or next to each row of gravestones in each block. Eastern hemlocks in blocks two, three, and five are spaced further apart with two to three hemlocks in each row, while blocks one and four have four or more per row that allow the tree branches from different trees to touch each other. The eastern hemlocks were planted around 1922 when the cemetery opened. The EHS infestation was not found until June 2004, when the first survey of this site was made while searching for potential field sites. Within the last two years, four trees have died, and EHS is believed to have played a role in their mortality.

Biltmore Estate (24.3 km^2) consists of forest, farmland, gardens, and the historic Biltmore House. Each urban block is located in or near a parking lot and extends toward the forested areas. Parking lots A, B, C, winery and hotel, and the bus area before the entrance to the estate comprised the five urban blocks. The forest blocks are located on top of a hill where the Biltmore Estate House can be viewed to the west and south of Parking Lot A. This area is one of the highest points on the property and the forest contains primarily hemlocks with tulip-poplar, pine, and oak interspersed among the hemlocks. A horse trail divides blocks one, two, and three (south side) from four and five (north side). The branch of this trail divides block one and two from each other. Block three is separated from block two by a trail that stops at a rail fence, and a white oak tree at the edge of the horse trail separates block four and five.

The construction on the Biltmore Estate House began in 1889, and the home was finished in 1895. During this time period, the gardens and forested areas were designed and trees and shrubs were planted. The house was opened to the public in 1930 and is still open today. The majority of the eastern hemlocks in the forested areas are at least 100 years old, although many of the eastern hemlocks in the urban (parking lots) were planted in more recent years.

Predator collections by beat sheet

Predators were collected using a standard (1 m^2) beat sheet by striking one branch three times from each of the four cardinal directions per tree to determine field

occurrence of EHS predators. This procedure was replicated for three trees in each of the five blocks for all four sites. The beat sheet was scanned for predators, and when discovered, they were placed into separate, labeled (site, block, tree, and direction) glass Fisherbrand® vials (6 dram) and placed in a cooler during warm sampling days for transport to the laboratory. Predators were identified in the laboratory or by specialists.

Beat sheet samples were collected monthly at Biltmore and Bays Mountain, but beat sheets were taken from Lynnhurst twice monthly. For the Lynnhurst site the two monthly samples were averaged for comparisons with the other sites. Predators were sampled from 11:00 am to 4:30 pm for each sampling day. From 15 September 2004 to 29 May 2006, beat sheet samples were each taken at Lynnhurst (2,520) and Biltmore urban and forest sites (2,520). Bays Mountain Park was sampled from 8 August 2005 to 20 May 2006 resulting in 600 beat sheet samples. Data for site, block, tree, cardinal direction, number of predators collected, different species collected, and date collected were recorded in Excel files for all predator species collected

Branch samples

At each site, five trees were randomly selected and sampled per block with two branch (30 cm) samples clipped from each tree resulting in 200 samples from all sites monthly. Each sample was placed in a 3.8 liter (one gallon) Ziploc® plastic bag, labeled (site, block, tree, sample, and date) and transported to the laboratory for processing. Samples were stored in a refrigerator until specimen counts could be made. Lynnhurst and Biltmore sites were sampled 15 times from 8 October 2004 to 28 April 2006 for a total of 2,250 samples. Bays Mountain Park was sampled nine times from 8 August 2005 to 10 April 2006 for a total of 450 samples. One hundred needles per each sample were counted for the 2,700 branch samples. Each count was randomly started from either the tip or base of the branch clipping with old and new growth. The numbers of adult female EHS, predator damage, and live predators for each sample were recorded on data sheets and in Excel files. Predator damage was defined as any part of the female scale that was missing parts or most of the test with ragged edges around the missing sections.

Analysis of data

For all ANOVA, the assumptions for parametric statistics were tested first using Shapiro-Wilk's statistic for normality and Levene's Test for Equality of Error Variances. Percent damage for predator damage was determined for branch samples. After 0.05 was added to all numbers, the natural log of predator damage by site was taken to correct for normality and variance inconsistencies (Zar 1999). After running an ANOVA for branch sample, dbh and beat sheet collection data, the Least Significant Difference method was used to test the significant differences in LS Means. The natural log was not applied to the dbh, infestation rating, or beat sheet collection data. The branch sample data were analyzed seasonally by dividing each season into three months of a year. Fall included the months of September, October, and November, and winter was December through February. Spring was March through May, and summer included June, July, and August. The two samples per month for the Lynnhurst site were averaged together rounded up to the nearest whole number for each month. All ANOVAs and tests of assumption were run using SAS 9.1. Multiple Chi-Square tests were used to analyze the predator collection data by species for site and direction using SPSS 14.0 for Windows.

Results

Sampling sites

Heavy populations of EHS were present at three of the four sites with infestation ratings exceeding 3.5 on a scale of 0-4 (Table 3). These sites are considered to be heavily infested, while the Bays Mountain Park site is moderately infested at this time. The Bays Mountain Park site had a significantly lower ($F = 24.09$, df = 3, $P < 0.0001$) infestation rating than the Biltmore or Lynnhurst sites. Because of the lower incidence of EHS and the time EHS was initially observed on the trees at the Bays Mountain Park site, this represents a relatively new invasion by the pest. The dbh at the Lynnhurst site was significantly higher ($F = 40.64$, df = 3, $P < 0.001$) than the dbh at the other three sites.

Table 3. Mean *Fiorinia externa* infestation ratings[1] (± SD, n = 1,000) and diameter breast height[2] (dbh) (± SD, n = 200) for eastern hemlocks at the four sampling sites.

Sites	Mean infestation rating ± SD	Mean dbh ± SD (cm)
Bays Mountain Park (Forest)	**2.26 ± 1.33b**	**25.86 ± 3.44 b**
Biltmore Estate (Forest)	**3.77 ± 0.51a**	**21.16 ± 2.50 b**
Biltmore Estate (Urban)	**3.61 ± 0.83a**	**23.80 ± 5.56 b**
Lynnhurst Cemetery (Urban)	**3.84 ± 0.41a**	**59.11 ± 5.70 a**

[1] infestation rating = 1 for 1-3 infested branches, 2 for 4-6 branches, 3 for 7-10 branches, and 4 for 11 or more infested branches (50 trees in each block, 20 blocks, 4 sites)
[2] dbh = 10 random trees in each block, 20 blocks, 4 sites

Eastern hemlocks are considered mature after 20 to 40 years in the open and from 30 to 50 years in areas with moderate light (Merrill and Hawley 1924). The average dbh for a 40-year-old tree in Tennessee is 4.8 cm, and the average dbh for a 100-year-old tree is 23.9 cm (Frothingham 1915, Fowells 1965). The trees in the two forest sites are about 100 years old, and the mean for both of these sites is close to the average for the region. In the two urban sites, there was a large difference between the mean dbh for the two sites. The dbh for the urban site at Lynnhurst was significantly higher ($F = 40.64$, df = 3, $P < 0.001$) than the urban site for Biltmore, and many trees in the parking lot areas of Biltmore were planted more recently than at Lynnhurst. The dbh between the two forest sites was higher at the Bays Mountain Park site, even though trees in both areas are about 100 years old. Some reasons for the differences between urban and forest sites could be that the urban areas receive more sunlight and fertilizer, which allows the trees to mature faster and have a greater dbh. The forest site at Bays Mountain Park had a higher dbh than the urban site at Biltmore, and the trees at Biltmore urban are much younger than those at Bays Mountain.

Predator collections by beat sheet

Six predaceous species were collected and identified during this study. These included five coccinellids: *Chilocorus stigma* (Say), *Harmonia axyridis* (Pallas) (native to Asia), *Rhyzobius lophanthae* (Blaisdell) (native to Australia), *Scymnillus horni* Gordon, *Scymnus loweii* Mulisant (native to Australia), and the neuropteran *Conwentzia pineticola* Enderlein (native to Europe). Predators collected from September 2004 through May 2006 were 312 adults (161 *S. horni*, 68 *R. lophanthae*, 26 *C. stigma*, and 7 *S. loweii*, 41 *C. pineticola*, and 9 *H axyridis)*, one pupa, and 154 beetle larvae (110 *R. lophanthae*, 8 *S. horni*, 34 *C. stigma*, 2 *H axyridis*). *Rhyzobius lophanthae* was the most abundant followed by *S. horni*, *C. stigma*, and *C. pineticola* (Fig. 2). *Harmonia axyridis* and *S. loweii* were the least abundant, representing about 2% each of all predators collected.

The highest numbers of specimens and species were collected from May through October in 2005 (Fig. 3). *Scymnillus horni* appears to have one generation, possibly two,

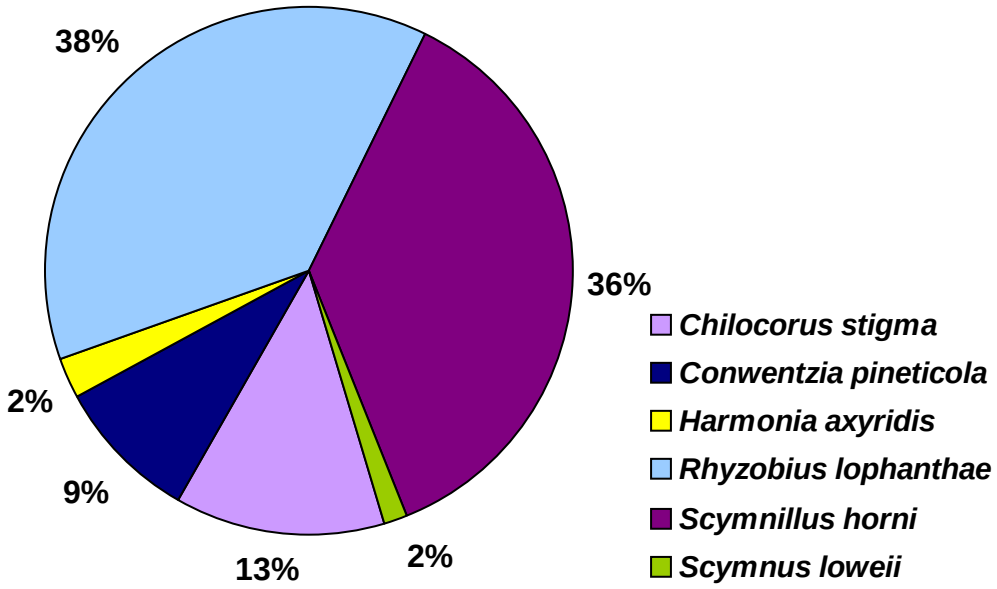

Fig. 2. Species composition of all field-collected predators from four test sites.

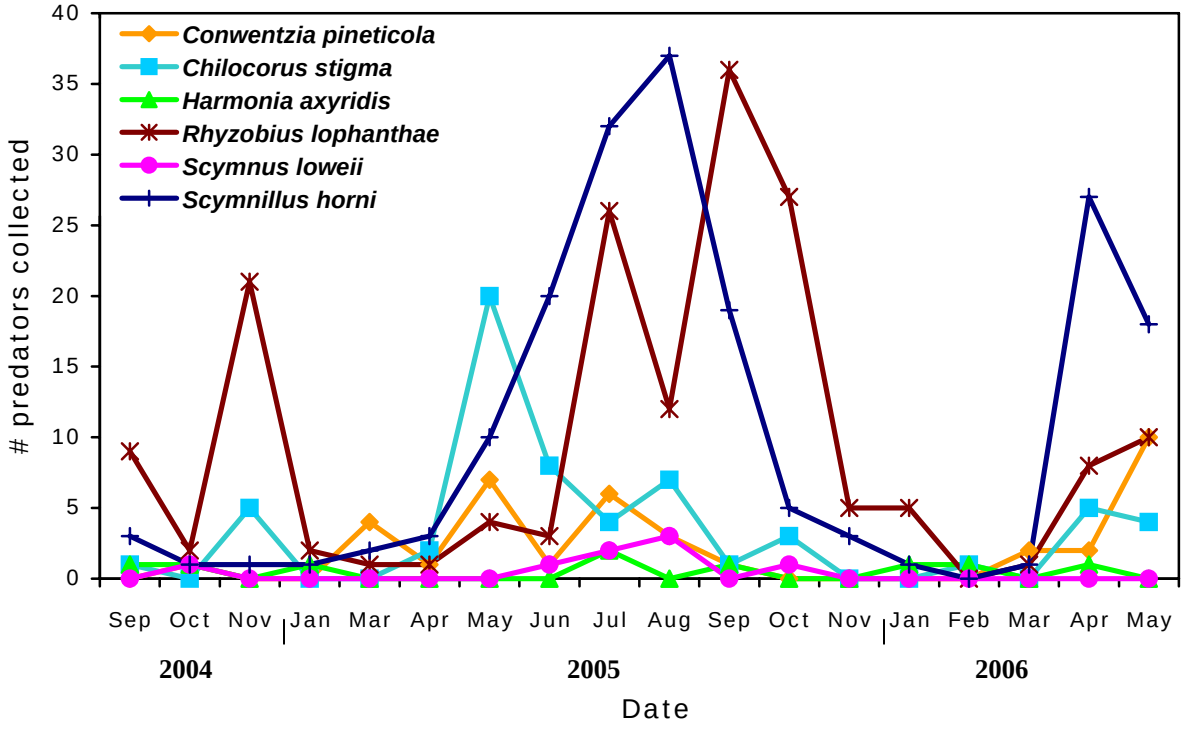

Fig. 3. Seasonality of all predaceous species collected from September 2004 to May 2006.

per year with peak collections between March and May (27) and from June to August (37). There was no previous information known about the life cycle or development of this species including how it overwinters. *Rhyzobius lophanthae* larvae and adults were present throughout the year and active during the winter months, when other predators are not present. It has multiple, overlapping generations annually. From field collections during this study, *R. lophanthae* had two to three generations with peak collections of specimens obtained in November (21), from June to August (26), and from September to October (36). This species was reported to have five to seven generations annually without diapause in warmer climates like Greece (Katsoyannos 1996, Rubstov 1952, Smirnoff 1950, Stathas 2000b). *Chilocorus stigma* was found during all but the coldest months of the year and had two to three generations with peak collections of specimens made in November (5), from April to June (20), from July to August (7), and from April to May (5) in Tennessee and North Carolina. Two generations annually were reported for this species in New York (DeBoo and Weidhaas 1976), and three generations were found in Florida (Muma 1955). In New York, this species is reported to overwintered in the duff underneath the trees as an adult and appeared on the first warm day (13°C) in March (Mayer and Allen 1983).

Scymnus loweii was collected during the summer in August (3) and fall in October (1), inferring one or two generations per year. *Harmonia axyridis* is reported to have two generations in Asia (Osawa 2000, Sakurai et al. 1992), North America (Koch and Hutchison 2003, LaMana and Miller 1996), and Europe (Ongagna et al. 1993), although four to five generations have been observed (Wang 1986, Katsoyannos et al. 1997). Insufficient numbers of specimens for this species were collected to accurately determine the generations per year. In the fall, they aggregate in cracks and crevices and go into a state of diapause as adults for most of the winter (Koch 2003). *Conwentzia pineticola* was active in the spring through the fall with peak collections of specimens made in March (4), May (7), July (6), and May (10) but was found in fewer numbers than the other species except *H. axyridis*. It could possibly have two or three overlapping generations per year in this region. This species overwintered as a pupa in a circular,

white cocoon attached to the bark of tree trunks or twigs (Collyer 1951). It primarily consumes different species of mites and their eggs (Collyer 1951).

Although predators of EHS were found at urban and forest sites, the number of species and combinations of species differed per site. The highest number of *S. horni* adults and larvae was collected at the Biltmore urban site (Table 4). Adult and larvae *C. stigma*, *R. lophanthae* larvae, and adult *C. pineticola* were found in the greatest abundance at Biltmore urban site. The highest number of predators was collected at the Biltmore urban site. Also, more specimens for each species were collected from urban sites than forest sites (Fig. 4). The fewest numbers of specimens were collected at the Bays Mountain forest site, however, the low numbers are a result of fewer collections made at the Bays Mountain forest site as well as the area only recently invaded by EHS. As such, *Scymnillus horni* was the only species collected at the Bays Mountain site, while *S. loweii* was found only at the Lynnhurst site.

Predators were found in all cardinal directions on eastern hemlocks collected from beat sheet samples (Table 5). Similar numbers of *C. pineticola* were collected from all cardinal directions of the hemlock trees. *Scymnillus horni* was most often found on the south, east, and north sides. Adult *R. lophanthae* were mainly found on the north side of the host tree, but the highest numbers of larvae were found on the west side of the trees. Although more specimens were found in certain directions, there was no significant association between direction and site preference that was independent of species for Biltmore forest ($X^2 = 8.854$, df = 12, $P = 0.758$), Biltmore urban ($X^2 = 9.924$, df = 12, $P = 0.623$), or Lynnhurst urban ($X^2 = 7.383$, df = 12, $P = 0.887$). An insufficient number of *Scymnus loweii* and *H. axyridis* were collected and could not be included in analysis. Observations on the location of specimens by site and direction infer that most species are fairly evenly distributed over all sites, except Bays Mountain where eastern hemlocks are lightly infested with EHS, and all four directions (Table 6). *Scymnillus horni* were most often found at Lynnhurst urban site on the south side of the tree, while *R. lophanthae* were collected most frequently from the north side of the tree at Biltmore urban site.

Table 4. Total number of predators collected monthly by beat sheet from two forest and two urban sites from September 2004 to May 2006.

Species	Forest		Urban		
	Bays Mtn*	Biltmore	Biltmore	Lynnhurst**	Total
Conwentzia pineticola	0	11	20	10	41
Chilocorus stigma	0	3	22	1	26
Chilocorus stigma larvae	0	3	31	0	34
Harmonia axyridis	0	2	5	2	9
Harmonia axyridis larvae	0	0	1	1	2
Rhyzobius lophanthae	0	3	57	8	68
Rhyzobius lophanthae larvae	0	17	92	1	110
Rhyzobius lophanthae pupa	0	0	1	0	1
Scymnillus horni	3	16	73	69	161
Scymnillus horni larvae	1	2	1	4	8
Scymnus loweii	0	0	0	7	7
Total	4	57	303	103	467

*** Bays Mtn. Forest site sampled 10 times (August 2005 to May 2005) compared to 21 times for the other three sites.**

**** Lynnhurst sampled twice per month and number was averaged to nearest whole number**

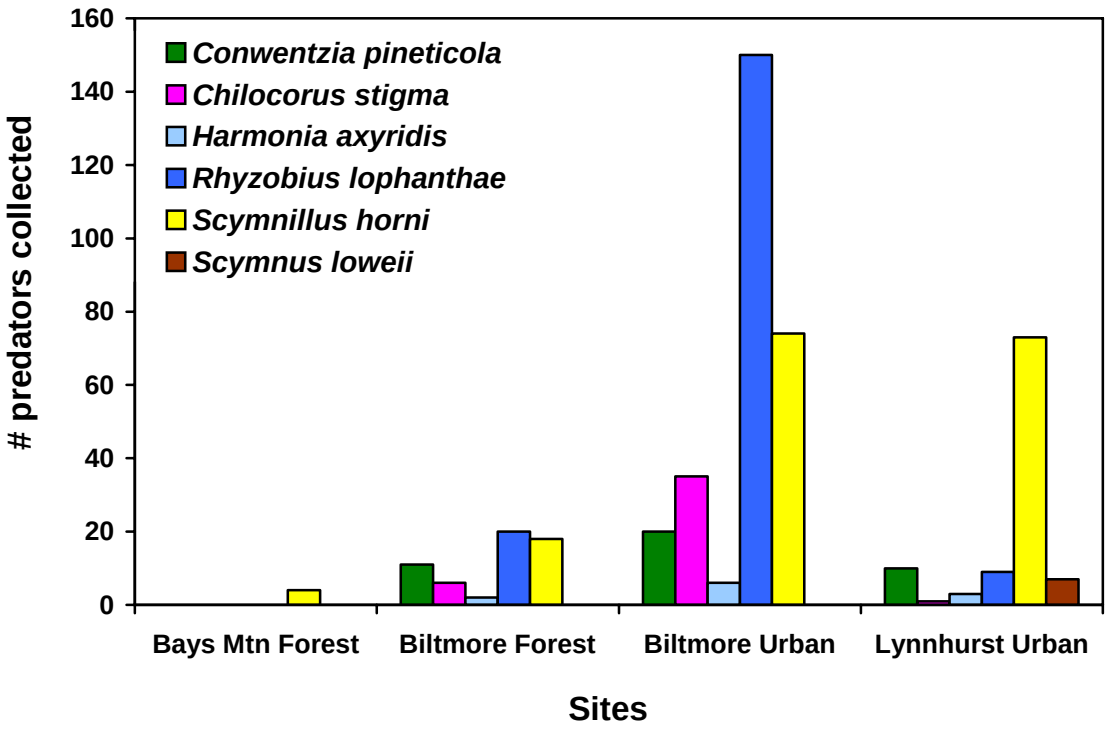

Fig. 4. Total number of larvae and adults per species collected monthly at four sites (two forest and two urban sites) from September 2004 to May 2006. (Bays Mtn. Forest site sampled 10 times (August 2005 to May 2005) compared to 21 times at other three sites)

Table 5. Number of specimens for predators of *Fiorinia externa* collected monthly from May 2005 to May 2006 using beat sheets in the four cardinal directions at four sites[1, 2] (two forest and two urban sites).

	Direction			
Species	**North**	**East**	**South**	**West**
Conwentzia pineticola	**5**	**7**	**8**	**5**
Chilocorus stigma	**7**	**1**	**5**	**5**
***Chilocorus stigma* larvae**	**10**	**8**	**10**	**5**
Harmonia axyridis	**1**	**1**	**2**	**2**
***Harmonia axyridis* larvae**	**0**	**0**	**1**	**0**
Rhyzobius lophanthae	**20**	**15**	**8**	**7**
***Rhyzobius lophanthae* larvae**	**24**	**15**	**17**	**26**
***Rhyzobius lophanthae* pupa**	**1**	**0**	**0**	**0**
Scymnillus horni	**43**	**34**	**40**	**30**
***Scymnillus horni* larvae**	**2**	**2**	**1**	**3**
Scymnus loweii	**1**	**3**	**1**	**2**

[1] Bays Mtn. Forest site sampled 10 times (August 2005 to May 2005) compared to 13 times for Biltmore Estate urban and forest sites.

[2] Lynnhurst sampled twice per month and number was averaged to nearest whole number

Table 6. The number of *Fiorinia externa* predator specimens (larvae and adults) per species by site and direction collected monthly from May 2005 to May 2006 using beat sheets in the four cardinal directions at four sites (two forest and two urban sites).

		Direction			
Site	**Species**	**North**	**East**	**South**	**West**
Bays Mtn Forest*	***Conwentzia pineticola***	**0**	**0**	**0**	**0**
	Chilocorus stigma	**0**	**0**	**0**	**0**
	Harmonia axyridis	**0**	**0**	**0**	**0**
	Rhyzobius lophanthae	**0**	**0**	**0**	**0**
	Scymnillus horni	**2**	**0**	**0**	**2**
	Scymnus loweii	**0**	**0**	**0**	**0**
Biltmore Forest	***Conwentzia pineticola***	**0**	**5**	**4**	**2**
	Chilocorus stigma	**1**	**3**	**1**	**1**
	Harmonia axyridis	**0**	**1**	**0**	**1**
	Rhyzobius lophanthae	**4**	**5**	**5**	**6**
	Scymnillus horni	**5**	**3**	**4**	**4**
	Scymnus loweii	**0**	**0**	**0**	**0**
Biltmore Urban	***Conwentzia pineticola***	**5**	**1**	**3**	**3**
	Chilocorus stigma	**16**	**6**	**14**	**9**
	Harmonia axyridis	**1**	**0**	**2**	**1**
	Rhyzobius lophanthae	**40**	**25**	**19**	**27**
	Scymnillus horni	**27**	**15**	**15**	**10**
	Scymnus loweii	**0**	**0**	**0**	**0**
Lynnhurst Urban**	***Conwentzia pineticola***	**2**	**1**	**1**	**2**
	Chilocorus stigma	**0**	**0**	**0**	**0**
	Harmonia axyridis	**0**	**0**	**1**	**0**
	Rhyzobius lophanthae	**1**	**0**	**1**	**2**
	Scymnillus horni	**10**	**17**	**21**	**15**
	Scymnus loweii	**1**	**3**	**1**	**2**

*** Bays Mtn. Forest site sampled 10 times (August 2005 to May 2005) compared to 13 times for the other three sites.**

**** Lynnhurst sampled twice per month and number was averaged to nearest whole number**

The total number of specimens collected from beat sheets was lower than many other studies conducted on EHS and *Cryptococcus fagisuga* Lindinger, beech scale (McClure 1979b, Mayer and Allen 1983), but it was similar to a forest survey for HWA predators with 147 predator specimens collected overall (Wallace and Hain 2000). Larva and adults were collected for all species except *C. pineticola* and *S. loweii*. The lower crown in the forest was harder to reach while conducting beat sheet sampling. Thus, higher predator populations may have been documented if the whole tree could have been sampled. Urban areas often had more dense branches much lower to the ground.

Branch samples

The average predator damage to EHS populations in the field was 8.28% (4.72 to 9.84%) for the four sampling sites. Predator damage averaged 9.84% at the Biltmore urban site, 9.65% at the Biltmore forest site, 6.16% at the Lynnhurst urban site, and 4.72% at the Bays Mountain Park forest site. Predator damage at the Lynnhurst urban site was significantly lower ($F = 47.23$, df $= 2,81$; $P < 0.0001$) than that at either Biltmore forest or urban, which were not significantly different ($F = 47.23$, df $= 2,81$; $P < 0.0001$) from each other. The lowest predator damage occurred at the Bays Mountain site (3.43) during August to December and the highest damage occurred at the Biltmore forest site (10.89) from January to April (Table 7). For all four sites, significantly lower ($F = 4.44$, df $= 3,69$; $P < 0.0065$) predator damage occurred in the summer than the other three seasons, which were not significantly different ($F = 4.44$, df $= 3,69$; $P < 0.0065$) from each other. No significant difference ($F = 1.66$, df $= 6,81$; $P = 0.1404$) was found for predator damage between Lynnhurst and Biltmore sites for all four seasons.

Mean predator damage for fall 2004 was significantly lower ($F = 8.35$, df $= 1,24$; $P < 0.0080$) from mean predator damage in 2005 for Biltmore urban, Biltmore forest, and Lynnhurst urban. For 2004 and 2005 predator damage, Biltmore urban and forest were not significantly different ($F = 15.32$, df $= 2,24$; $P < 0.0001$) from each other, but Lynnhurst urban was significantly lower ($F = 15.32$, df $= 2,24$; $P < 0.0001$) than both Biltmore sites. During 2005 and 2006, predator damage at Biltmore urban and forest sites did not differ significantly ($F = 44.03$, df $= 3,59$; $P < 0.0001$) from each other, but it was

Table 7. Predator damage to *Fiorinia externa* collected monthly at two urban and two forest sites from October 2004 to April 2006.

Sites	Sampling months	No. EHS** with predator damage	Total no. EHS	Percent predator damage
Lynnhurst Urban 2004	Oct.-Dec.	970	18,852	5.15
Lynnhurst Urban 2005	Apr.-Dec.	4,437	70,795	6.27
Lynnhurst Urban 2006	Jan.-Apr.	1,854	28,133	6.59
Biltmore Urban 2004	Oct.-Dec.	1,422	16,034	8.87
Biltmore Urban 2005	Apr.-Dec.	6,611	66,027	10.01
Biltmore Urban 2006	Jan.-Apr.	2,811	28,182	9.97
Biltmore Forest 2004	Oct.-Dec.	1,242	14,941	8.31
Biltmore Forest 2005	Apr.-Dec.	6,081	64,436	9.44
Biltmore Forest 2006	Jan.-Apr.	2,978	27,355	10.89
Bays Mtn. Forest 2005*	Aug.-Dec.	274	7,996	3.43
Bays Mtn. Forest 2006*	Jan.-Apr.	620	10,946	5.66

*** Bays Mtn. Forest site sampled 9 times compared to 16 times for the other three sites.**

**** *Fiorinia externa* Ferris, elongate hemlock scale.**

significantly higher ($F = 44.03$, df = 3,59; $P < 0.0001$) at Lynnhurst urban and Bays Mountain forest sites. For the same time period, predator damage at Lynnhurst urban site was significantly lower ($F = 44.03$, df = 3,59; $P < 0.0001$) than the Biltmore sites but higher than Bays Mountain, and Bays Mountain forest also was significantly lower ($F = 44.03$, df = 3, 59; $P < 0.0001$) from the three sites. There was a site by season interaction for 2005 and 2006 using spring (March through May) and winter (December through February) which all sites had in common (Fig. 5). The predator damage in spring at Bays Mountain and Lynnhurst sites were not significantly different ($F = 3.79$, df = 3,59; $P < 0.0148$) from each other or the Lynnhurst urban site for winter but was significantly different ($F = 3.79$, df = 3,59; $P < 0.0148$) from the two Biltmore sites. Damage levels at the two Biltmore sites did not differ significantly ($F = 3.79$, df = 3,59; $P < 0.0148$).

Predator damage during the winter differed significantly ($F = 6.46$, df = 9,60; $P < 0.0001$) among all four sites with the lowest (4.41) percent damage occurring at the Bays Mountain forest site and the highest (11.85) at the Biltmore forest site (Table 8). During the spring, damage levels were lowest at the Bays Mountain forest and Lynnhurst urban sites. The damage levels were similar at the Biltmore urban and forest sites. Damage levels during the summer were significantly different ($F = 6.46$, df = 9,60; $P < 0.0001$) among the four sites. The lowest percent damage for the summer occurred at the Bays Mountain forest site (1.46) and highest at the Biltmore urban site (9.78). Fall damage by predators did not differ significantly ($F = 6.46$, df = 9,60; $P < 0.0001$) at the Biltmore urban and forest sites. However, damage at the latter sites was significantly higher ($F = 6.46$, df = 9,60; $P < 0.0001$) than at the Lynnhurst urban and Bays Mountain forest sites.

Within each of the four sites, seasonal variation occurred over the sampling period (Fig. 6). For the Bays Mountain site, the predator damage was significantly different ($F = 6.46$, df = 9,60; $P < 0.0001$) for all four seasons. Mean percent predator damage during spring and fall were significantly different ($F = 6.46$, df = 9,60; $P < 0.0001$) with winter the lowest and summer the highest for Biltmore forest. Predator damage was not significantly different ($F = 6.46$, df = 9,60; $P < 0.0001$) among the seasons at Biltmore urban. At Lynnhurst urban, damage during the summer was significantly lower ($F = 6.46$, df = 9,60; $P < 0.0001$) than the other three seasons.

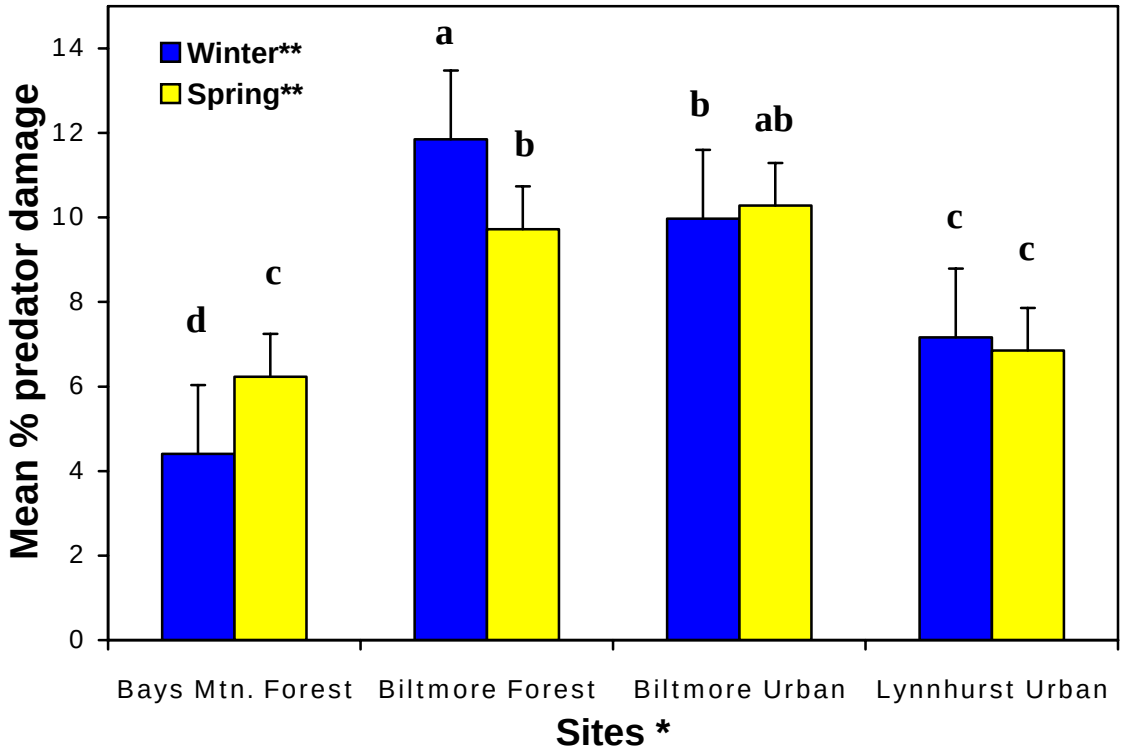

Fig. 5. Mean percent (± SE) predator damage on Fiorinia externa at four sites from 2005 and 2006.
*** Means with same letters are not significantly different among all sites (*a* = 0.05).**
****Winter = December through February & Spring = March through May**

Table 8. Mean percentage (± SD) of predator damage to *Fiorinia externa* by season among all four sites (n = 2,700).

Sites	Season***	Mean percentage of predator damage ± SD*
Bays Mtn. Forest**	**Winter**	**4.41 ± 0.047 g**
	Spring	**6.23 ± 0.053 ef**
	Summer	**1.46 ± 0.032 i**
	Fall	**3.52 ± 0.048 h**
Biltmore Forest	**Winter**	**11.85 ± 0.063 a**
	Spring	**9.72 ± 0.056 b**
	Summer	**7.63 ± 0.040 c**
	Fall	**9.50 ± 0.052 b**
Biltmore Urban	**Winter**	**9.97 ± 0.072 b**
	Spring	**10.28 ± 0.066 ab**
	Summer	**9.78 ± 0.059 b**
	Fall	**9.74 ± 0.062 b**
Lynnhurst Urban	**Winter**	**7.16 ± 0.041 cd**
	Spring	**6.85 ± 0.042 cde**
	Summer	**4.98 ± 0.029 f**
	Fall	**6.09 ± 0.037 def**

*** Means with the same letters are not significantly different (*a* = 0.05).**
**** Bays Mtn. Forest site sampled 9 times compared to 16 times for the other three sites.**
***** Winter = December through February, Spring = March through May, Summer = June through August, Fall = September through November.**

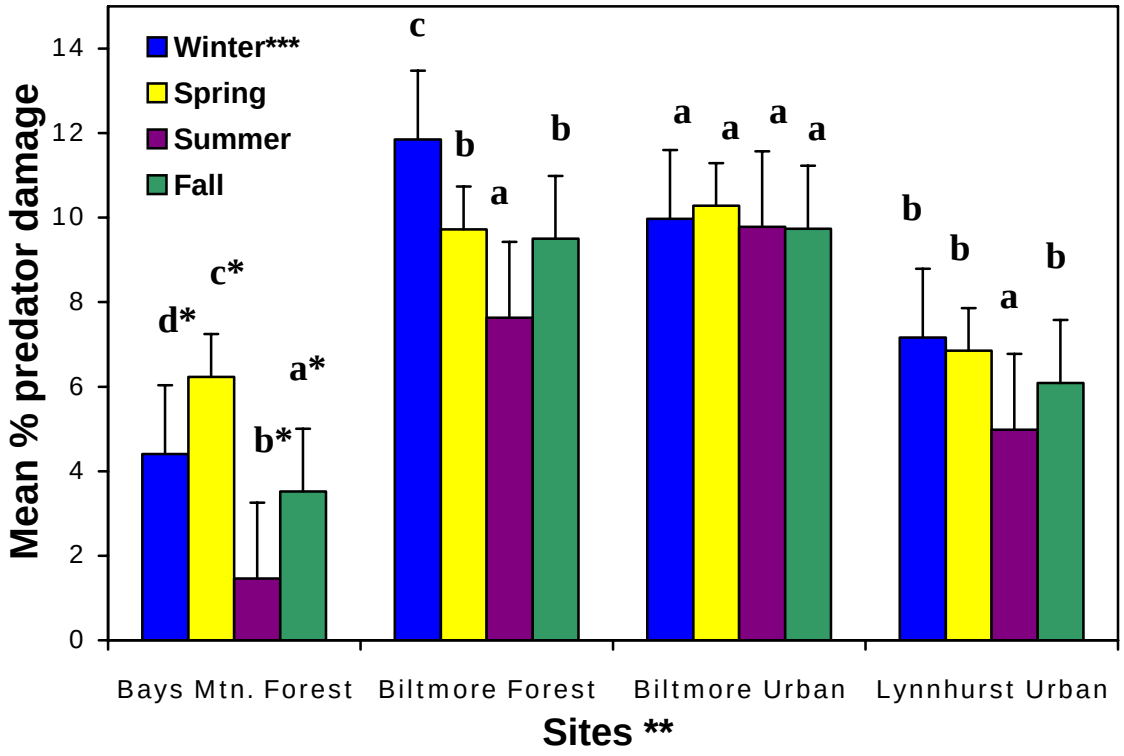

Fig. 6. Mean percent (± SE) predator damage to *Fiorinia externa* for all four sites and seasons.
*** Bays Mtn. Forest site was sampled 9 times compared to 16 times for the other three sites.**
**** Means with same letters are not significantly different within each site (*a* =0.05).**
***** Winter = December through February, Spring = March through May, Summer = June through August, Fall = September through November.**

Overall, Biltmore urban and forest sites had the most predator damage to EHS from the collected branch samples and had the most site similarities. Biltmore urban had the most constant predator damage, and Bays Mountain had the most fluctuations for all seasons. Bays Mountain and Lynnhurst shared similarities in predator damage for spring. Biltmore forest and urban sites had the highest field predator damage (9.84 and 9.65 %, respectively).

Discussion

Six native and introduced predator species were collected from two urban and two forest sites from 2004 to 2006 in eastern Tennessee and western North Carolina. Two of the five coccinellid species, *S. horni* and *R. lophanthae*, represented new state records for Tennessee, and the collection of *S. loweii* denoted new county records for eastern Tennessee. The heavy EHS infestations at Lynnhurst urban, Biltmore forest, and Biltmore urban sites supported a higher number of predators than the Bays Mountain Park site, which had a light to moderate EHS infestation and low numbers of predators. The Bays Mountain site represents a more recent EHS infestation than the three other sites, but it is possible that a higher and more diverse population of predators will occur over time as the population levels increase. It may take longer for different predator species to establish at this site because of its remote location, but the release of native or introduced predators would help to increase the predator populations.

Predators were collected at all sites, but the numbers and species collected varied for each site. Seasonal differences occurred for the predators with less collected during the winter and more collected in the spring and summer months, as expected. For all of the sites, more predators could have been present but were not collected because of the lack of stratification for the beat sheet samples and only sampling once a month. McClure (1979c) found that *C. stigma* was collected in higher numbers in the middle and upper canopy. However, the heaviest EHS infestations were located in the lower canopy, and many branches in the lower canopy on taller trees could not be reached for sampling. The

Biltmore urban site had the highest total number of predators collected, and one reason for this could be more available branches for sampling. The differences between the urban and forest sites for predator collection may be due to fewer branches available for sampling at the forest sites.

Predator damage to EHS in the field occurred throughout the year with some seasonal differences. Biltmore urban and Lynnhurst urban had less variation in seasonal predator damage than the forest sites. This variation could be an effect of random sampling or clumping of predators in certain areas and not other areas. These established predators damaged 3.4 to 10.9% of EHS. The damage recorded and predators collected would not be sufficient by themselves to control the EHS infestations, but they could be augmented by the additional releases of selected predators and by the parasitoid, *Encarsia citrina* (Craw), that was found to damage 17.9 to 41.3% of EHS (Lambdin et al. 2005). The augmentation of the existing predator populations may help increase predator damage and help lower the EHS infestation levels and prevent tree mortality. At present, extensive mortality of the eastern hemlock resulting from the EHS infestation at the sites has not occurred. The occurrence of these natural enemies may provide a stabilizing effect on the pest populations.

III. Behavior, Consumption, and Competition of Elongate Hemlock Scale Predators

Introduction

The initial phase of biological control includes research into fundamental aspects of taxonomy, biology, physiology, genetics, ecology and demography, behavior, culture methods, and nutrition (DeBach 1964). The role of predaceous insects has often been underestimated, but more focus should be on predators because of the considerable benefits from practical applications (Thompson 1929, Doutt and DeBach 1964). Several of the most successful examples of biological control were achieved by using predaceous species (Doutt and DeBach 1964). The most famous example was the use of the coccinellid, *Rodolia cardinalis* (Mulsant), against the cottony cushion scale, *Icerya purchasi* Maskell, that saved the citrus industry in California (Doutt 1964b). Specialist predators locate specific prey without distraction by the presence of other prey, and these predators are more appropriate for exotic introductions and may not adversely effect native predators (Symondson et al. 2002).

Assemblages or guilds of generalist predators can effectively suppress populations of indigenous and exotic pests (Sunderland 2001, Sunderland et al. 1997, Van Driesche and Bellows 1996). The work of DeBach (1946) and Ehler (1977) provided examples of generalist predators that more effectively controlled pests than specialist predators (Symondson et al. 2002). Biological control theory and applications suggest that generalist predators can be effective control agents, and assemblages of generalist predators reduced pests and yield loss in field studies (Symondson et al. 2002). Pesticides have caused the disruption of generalists, which led to a rapid decrease in control of pests, resurgence of pests, and new secondary pests (Settle et al. 1996). Local pest populations can be driven to extinction by generalists without a decline in the predator numbers, and these generalists will consume other nonpest prey and prevent the pest from re-entering the system (den Boer 1982). Specialist populations suffer when pest

populations are periodically depressed by other factors, but generalists can maintain their populations by feeding on other prey (Doutt and DeBach 1964). For most control projects, the establishment of a single control agent was more successful than multiple agents (Denoth et al. 2002).

Predators are large in size relative to their prey and require multiple prey individuals to complete development (Doutt 1964a, Hagen et al. 1976, Miller and Davidson 2005). The immature stages are free-living and predatory, and many species are predaceous as nymphs and adults (Doutt 1964a, Hagen et al. 1976, Obrycki et al. 2006). Effective predators exhibit some prey specificity, a higher fecundity rate than their prey, and tolerance of abiotic factors similar to the prey (DeBach and Rosen 1991, Hassell and May 1986). Prey selection by predators involves four steps: habitat selection, identifying prey individuals on the plant, prey acceptance, and ability of the predator to feed on the prey (Hoy 1994). From observations in the laboratory and other artificial situations, predators responded to physical and chemical cues from the prey, host plant, and from an interaction of the two (Hoy 1994). Larval predators have assorted ways to locate and recognize their prey including phototactic or geotactic responses, vision, olfaction, sound or vibration detection, and contact (Hodek 1993).

The searching behavior of larvae and adult predators is important to understanding predator-prey interactions in biological control (Obrycki et al. 2006). Predator diet results from various physiological, behavioral, and ecological factors which include accessibility of certain types of prey, foraging behavior, suitability of prey, and the danger of predation (Price 1984, Endler 1991, Begon et al. 1996). After the predator discovers the prey, it pursues, subdues, and consumes it (Obrycki et al. 2006). Numerous morphological and physiological factors influence prey acceptance (Hagen 1987), and size of the prey is a principal physical factor (Sih 1987, Sabelis 1992). After the preliminary contact with possible prey, the characteristics of the cuticle or wax influence the response of the predator to the prey. Female predators often lay eggs close to their prey (Obrycki et al. 2006).

Functional responses can be modified by intraspecific interactions between predators that are affected by predator density, interference, and cannibalism (Nilsson

2001). Intraspecific and interspecific competition plays an important role in communities, and studies using species that are taxonomically or ecologically closely related contribute greatly to data interpretation (Price and Waldbauer 1994). Larger species of lady beetles feed on scale insects, mealybugs, aphids, and whiteflies (Hodek 1973, Hoy 1994). Most Neuroptera are predators that feed on scale insects, aphids, mealybugs, mites, and other small arthropods (Hoy 1994).

Fiorinia externa Ferris, elongate hemlock scale (EHS), was introduced into the United States on exotic hemlocks around 1910 in New York City from Japan and became established on native eastern hemlock (Sasscer 1912). EHS has recently invaded eastern hemlocks in forests within North Carolina and Tennessee (Lambdin et al. 2005). First instars of EHS settle on the underside of hemlock needles, insert mouthparts into the needle, and extract fluid from mesophyllic cells. Their feeding causes discoloration and premature dropping of needles, limb-dieback, and occasionally tree mortality after extended infestation (McClure 1980a). EHS has become a major pest of eastern hemlocks in the northeastern United States that weakened or killed trees in forested areas and ornamental plantings (McClure 1977b). Established EHS predators were found in the northeastern United States (McClure 1979b), but no consumption or behavioral studies were done on those species. As populations of EHS explode in the southeastern United States, natural enemies such as predators should be evaluated to suppress this exotic pest. The objective of this study was to evaluate development, survivability, consumption, intraguild competition, and feeding behavior of field-collected coccinellid and coniopterygid predators on EHS.

Materials and methods

Predator collections by beat sheet

Predators were collected using a standard (1 m^2) beat sheet by striking one branch three times from each of the four cardinal directions per tree to collect EHS predators. This procedure was replicated for three trees in each of the five blocks for all four sites

(5,640 total samples). The beat sheet was scanned for predators, and when discovered, they were placed into a separate, labeled (site, block, tree, and direction) glass Fisherbrand® vial (6 dram) and placed in a cooler during warm sampling days for transport to the laboratory. Predators were identified in the laboratory or by specialists. Other collections were made in an area unused in the regular monthly sampling at the Lynnhurst site to supplement predator numbers for testing. Laboratory tests were conducted using mainly field-collected predators *(Rhyzobius lophanthae* (Blaisdell)*, Scymnillus horni* Gordon, *Chilocorus stigma* (Say), *Harmonia axyridis* (Pallas), *Scymnus loweii* Mulsant, and *Conwentzia pineticola* Enderlein) to determine food consumption, development, survivability, feeding behavior, and intraguild competition for predators of EHS.

Predator sources

Specimens of *R. lophanthae* was established from specimens obtained from Green Methods Company were used to supplement the laboratory tests. Predators were maintained in Quarpack® 113.40 gram containers (7 cm tall, 5.5 cm wide) with Floralite® floral-foam at the bottom until needed for comparative tests. Each container had two pieces of gauze (4 cm long, 2 cm wide) for beetles to lay eggs on top of floral foam (one piece on either side of the branch), a 1 cm damp cotton ball for a water source, and ventilated polyester mesh (2.5 cm) in the center of each lid. Each container (10 total) held 5-10 adults on one EHS-infested clipping (3.81 cm long) and placed into the Floralite® floral-foam in the bottom one-third of the container maintained at 21°C in the laboratory. Adults were used to supplement field-collected *R. lophanthae* in consumption, behavioral, hemlock woolly adelgid consumption , and fecundity experiments.

Predator consumption

Predator consumption was conducted in the laboratory at 21°C in Fisherbrand® Petri dishes (6 cm) with a piece of damp Whitman® filter paper (4.25 cm). One drop of water on the filter paper from a plastic pipet (1 ml) was used every 2 to 3 d to maintain humidity in each dish, and wet piece (0.5 cm) of cotton was placed on the filter paper as a

water source for the predator. Predators were provided an infested hemlock branch (4 cm) with a low (5-10) or high (15-20) number of adult female and immature EHS that was placed on top of the damp filter paper. The same number of EHS was provided weekly, and each individual was monitored daily until death. Each dish was labeled with the specimen number and placed in rows by species on the laboratory counter. The species of adult predators used were *R. lophanthae* (44), *S. horni* (122), *C. stigma* (14), *H. axyridis* (5), *S. loweii* (11), and *C. pineticola* (29). The larval predators used were *R. lophanthae* (44), *S. horni* (8), and *C. stigma* (26). Specimens for each species were arranged in a complete randomized block design with 18 blocks replicated 8 to 122 times. Species, larva or adult, specimen number, females and nymphs provided each week, and weekly consumption recorded.

The location of predator damage to adult female EHS was recorded during consumption tests. The species of adult predators used were *R. lophanthae* (26), *S. horni* (32), *C. stigma* (20), *S. loweii* (10), and *C. pineticola* (10). Each individual specimen for each species was considered a replicate for the complete randomized block design. An adult female scale with eggs was divided into three sections (anterior, medial, and posterior) with one-third of the scale in each section. The anterior end of the scale contained the female scale inside the test and the old second instar test attached to the top of the adult female test, and the medial section began where the adult female scale ended and the eggs or chorion started. The posterior end included the eggs and the open end of the test where the crawlers emerge from the female.

Behavioral feeding response test

Predator behavior and consumption tests were performed with a single adult of *R. lophanthae*, *S. horni*, *C. stigma*, or *S. loweii*. Each test was replicated five times for two prey densities per species. Food was withheld for 24 h prior to assessment tests. The predator was placed in a Fisherbrand® Petri dish (9 cm) that was placed on top of an Easi-Grid® system (for measuring distance from predator to branch), and these tests were completed at 21°C. Each Petri dish contained a piece of Whitman® filter paper (4.25 cm) with one drop of water from a plastic pipette (1 ml) for moisture and an infested hemlock

branch (4 cm) with a counted amount of adult female and immature EHS placed on top of the damp filter paper. A hemlock branch with five female scales with eggs and five nymphs or 15 female scales with eggs and 15 nymphs were placed in the center of the dish 22 mm away from the predator. Data for each observation were recorded for 30 minutes. Specimen number, species, number of prey offered, prey recognition time, recognition distance, successful/unsuccessful attack, recognition type, time feeding, attack another prey, new attack time, total prey consumed, total feeding time, attack location on scale, and percent of scale attacked were recorded for each test. Observations on searching and feeding behavior for each predator also were recorded. The three recognition types were random (no pattern), zigzag (z-shape), and circling (inward spiral) as a predator searched for prey.

Predator competition

Four adult predators, *R. lophanthae*, *S. horni*, *S. loweii*, and *C. stigma*, were tested in combinations of two or three species at a time. The combinations were *R. lophanthae*-*R. lophanthae*, *R. lophanthae*-*S. horni*, *R. lophanthae*-*S. horni*-*S. loweii*, and *R. lophanthae*- *S. horni*-*C. stigma*. For each trial, adult predators were starved for 24 h and then provided with 5-10 or 15-20 female adult EHS and 5-10 or 15-20 nymphs. Each Fisherbrand® Petri dish (9 cm) contained a piece (4.25 cm) of Whitman® filter paper in the center of the dish and an infested hemlock (4 cm) branch with a counted amount of adult female and immature EHS placed on top of the damp filter paper. One drop of water from a plastic pipette (1 ml) was used to provide moisture in each dish. Specimens were observed immediately after being placed in the Petri dish (10 min) and for 10 min each h for 8 h, and then left overnight and observed again for 10 min per h for 8 h. Tests were performed at room temperature (21°C). To place the predators at equal distances from the branch, the dish was placed on top of an Easi-Grid® system to measure distance. Each predator was on a different square in the grid 20 mm from the hemlock branch. Each combination was replicated five times. Specimen number, species, combination, number of prey offered, recognition time, recognition distance, successful/unsuccessful attack, recognition type, time feeding, time between attacks, new attack time, total prey

consumed, and total feeding time were recorded. Observations on searching, feeding, and competitive behavior for each combination of predators were also recorded.

Hemlock woolly adelgid (HWA) consumption

The consumption of *Adelges tsugae*, hemlock woolly adelgid (HWA), by EHS predators was determined, since HWA is an invasive species on eastern hemlock and a competitor of EHS for tree resources in the field. This test was conducted using adult *R. lophanthae* and *S. horni* at 21°C. Each Fisherbrand® Petri dish (6 cm) contained a piece (4.25 cm) of Whitman® filter paper in the center of the dish and an infested hemlock branch (4 cm) with a previously recorded amount of adult female and immature HWA placed on top of the filter paper. One drop of water from a plastic pipette (1 ml) was used every 2 to 3 d to maintain humidity in each dish, and a wet piece (0.5 cm) of cotton was placed on the filter paper as a water source for the predator. The consumption of HWA was determined for 10 individuals of each species of EHS predators. Each individual was fed a low (five) or high (15) number of adult female adelgids and settled nymphs (1st instar). The same number of HWA was provided weekly, and the branch was checked weekly. The predator was placed in a sterile Petri dish with a new HWA-infested branch and new damp filter paper in it weekly. Data recorded were the number of damaged/eaten HWA females and nymphs, predator species, number of adelgid females and nymphs provided, and dates tested.

Female egg laying behavior

One male and female *R. lophanthae* were placed in a Fisherbrand® Petri dish (6 cm) with damp Whitman® filter paper (4.25 cm) and an infested hemlock branch (4 cm) with 20 female EHS and 20 nymphs. One drop of water on the filter paper from a plastic pipette (1 ml) was used every 2 to 3 d to maintain humidity in each dish, and a wet piece (0.5 cm) of cotton was placed on the filter paper as a water source for the predator. The pair was observed to see if copulation occurred, and after 48 h, the male was removed from the Petri dish and placed into the colony. Tests were performed at room temperature (21°C) using five pairs with three replicates. The branch and dish were checked daily for

egg production, and the eggs were removed using a fine hair paintbrush and placed into a separate dish when found. The old branch and dish were discarded each week and replaced with a fresh branch with the same number of EHS specimens. Data recorded were species collected, specimen number, number of EHS provided and eaten, date eggs laid, number of eggs laid, location of egg, and dates of test.

Analysis of data

ANOVA and the assumptions for parametric statistics were tested first using Shapiro-Wilk's statistic for normality and Levene's Test for Equality of Error Variances SAS 9.1. Recognition time was analyzed for behavioral feeding response data using an ANOVA, and the Least Significant Difference method was used to test significant differences between Least Squares Means among the species tested. After 0.05 was added to all numbers, the natural log of females and nymphs eaten for behavioral feeding response data was taken to correct for normality and variance inconsistencies (Zar 1999) and analyzed using ANOVA. The Pearson Chi-Square test was used to analyze attack success or failure, recognition type, attack location, and re-attack for the functional response and predator damage location. Pearson Correlation was used to compare relationships between feeding and egg laying for fecundity data. All correlations and nonparametric test were run using SPSS 14.0 for Windows.

Results

Predator consumption

Adult consumption

When adult predators were provided EHS as their food source in the laboratory, the highest numbers of EHS (Table 9) were consumed by *C. stigma*, *R. lophanthae*, *S. horni*, and *S. loweii*, ranked respectively. The fewest numbers of EHS were consumed or damaged by *C. pineticola* and *H. axyridis*. No significant differences ($F = 13.381$, df = 5, $P \leq 0.0001$) in the mean percent of immatures and adult females eaten occurred between

Table 9. Mean percent (± SD) of adult female and immature *Fiorinia externa* Ferris consumed by field collected adult predators (tested at 21º C).

Species	# tested	Mean percent* eaten ± SD		
		Adult females **	immature scales**	Total EHS**
Conwentzia pineticola	29	2.76 ± 0.070 e	14.46 ± 0.198 c	8.57 ± 0.099 cd
Chilocorus stigma	14	32.22 ± 0.179 a	28.45 ± 0.235 ab	36.83 ± 0.172 a
Harmonia axyridis	5	0.25 ± 0.006 de	7.22 ± 0.085 c	3.89 ± 0.041 d
Rhyzobius lophanthae	44	11.26 ± 0.132 b	37.51 ± 0.225 a	25.98 ± 0.158 a
Scymnillus horni	122	5.48 ± 0.088 cd	23.97 ± 0.183 b	15.97 ± 0.115 b
Scymnus loweii	11	5.66 ± 0.038 bc	17.84 ± 0.144 bc	12.96 ± 0.089 bc

*** Percent = the number of scales consumed divided by the number of scales offered**
**** Numbers followed by the same letters in a column are not significantly different (*a* =0.05).**

C. stigma and *R. lophanthae*, but their consumption was significantly higher ($F = 13.381$, df = 5, $P \leq 0.0001$) than the other four species. However, the recorded percent of adult female EHS consumed by *C. stigma* was significantly greater ($F = 13.381$, df = 5, $P \leq 0.0001$) than that consumed by *R. lophanthae*. No significant differences ($F = 13.381$, df = 5, $P \leq 0.0001$) were noted for mean percent total consumption for *S. loweii* and *S. horni*. The mean percent eaten by *C. pineticola* and *S. loweii* differed significantly ($F = 13.381$, df = 5, $P \leq 0.0001$), and those consumed by *C. pineticola* and *H. axyridis* were not significantly different ($F = 13.381$, df = 5, $P \leq 0.0001$).

Adult *C. stigma* consumed the highest mean percent of adult female EHS and differed significantly ($F = 16.946$, df = 5, $P \leq 0.0001$) from the other five species tested. *Rhyzobius lophanthae* and *S. loweii* consumption rates for adult female EHS were not significantly different ($F = 16.946$, df = 5, $P \leq 0.0001$) although *R. lophanthae* consumed almost twice the adult females, and *S. horni* and *S. loweii* were not significantly different ($F = 16.946$, df = 5, $P \leq 0.0001$) for adult than each other. No significant differences ($F = 16.946$, df = 5, $P \leq 0.0001$) occurred for mean consumption of female EHS between *H. axyridis* and *S. horni* or *C. pineticola* and *H. axyridis*. For the mean percent of nymphs eaten, *C. stigma* and *R. lophanthae* were not significantly different ($F = 6.644$, df = 5, $P \leq 0.0001$) from each other, but they were significantly higher ($F = 6.644$, df = 5, $P \leq 0.0001$) from *H. axyridis* and *C. pineticola*. In addition, *S. loweii*, *S. horni*, and *C. stigma* are not significantly different ($F = 6.644$, df = 5, $P \leq 0.0001$) from each other in the consumption of nymphs. Neither did *H. axyridis*, *S. loweii*, and *C. pineticola* differ significantly ($F = 6.644$, df = 5, $P \leq 0.0001$) from each other.

All of the predators, except *C. stigma*, were more likely to consume immature EHS than adult females. *Scymnillus horni* consumed less total number of scales than *C. stigma* or *R. lophanthae*, but more than the other species. *Harmonia axyridis* is primarily an aphid or adelgid predator, so it is not surprising that it did not consume many scales. *Conwentzia pineticola* is reported to mainly feed on mites, but it did consume scale when not given a choice. *Scymnus loweii* is a generalist that usually eats aphids, which explains the low number of scales it consumed. Using a combination of *C. stigma*, *R. lophanthae*,

and *S. horni* would ensure that immature and adult female EHS were consumed. The other three species of predators may consume EHS when preferred prey is absent.

Larval consumption

Chilocorus stigma consumed the highest mean percent of adult females and total scales but consumed the lowest mean percent of nymphs (Table 10). *Rhyzobius lophanthae* consumed the highest mean percent of EHS nymphs and the second highest percent of adult females and total number of EHS. *Scymnillus horni* had the lowest consumption for adult females and total number of specimens, but it was second for the number of nymphs consumed. No significant differences ($F = 0.602$, df = 2, $P = 0.550$) occurred among the three coccinellid species for mean total EHS consumed. The mean adult female EHS consumption for *C. stigma* was significantly higher ($F = 10.262$, df = 2, $P \leq 0.0001$) than the *R. lophanthae* and *S. horni*, which were not significantly different ($F = 10.262$, df = 2, $P \leq 0.0001$) from each other. The mean percent of nymphs eaten by *R. lophanthae* and *S. horni* did not differ significantly ($F = 14.842$, df = 2, $P \leq 0.0001$), but *C. stigma* was significantly lower ($F = 14.842$, df = 2, $P \leq 0.0001$) than the other two species. While larvae of *C. stigma* consumed mostly adult females, *R. lophanthae* and *S. horni* mainly consumed immatures.

Location of predator damage

Five of the six predators consumed different areas of adult female EHS (Table 11) during consumption tests. Occasionally, a predator consumed more than one area but not the entire adult female. *Conwentzia pineticola* attacked the left or right sides of female adult EHS ($X^2 = 73.092$, df = 16, $P \leq 0.0001$) and had the least attacks on the posterior end of the scale. Feeding on a whole female EHS occurred more frequently ($X^2 = 73.092$, df = 16, $P \leq 0.0001$) for *C. stigma* and the anterior section and sides were consumed the least. *Rhyzobius lophanthae* fed more often on the medial and anterior areas ($X^2 = 73.092$, df = 16, $P \leq 0.0001$) than posterior area. The medial and the posterior section were the most frequently consumed by *S. horni*, and the entire scale was consumed the least number ($X^2 = 73.092$, df = 16, $P \leq 0.0001$) of times. The sides were more often ($X^2 = 73.092$, df = 16, $P \leq 0.0001$) consumed by *S. loweii* than other areas.

Table 10. Mean percent (± SD) of adult female and immature *Fiorinia externa* Ferris consumed by field collected coccinellid larvae (tested at 21º C).

Species	# tested	Mean percent* eaten ± SD**		
		Adult females	Immature scales	Total EHS
Chilocorus stigma	26	26.02 ± 0.227 a	5.26 ± 0.121 b	26.35 ± 0.225 a
Rhyzobius lophanthae	44	9.54 ± 0.126 b	33.42 ± 0.255 a	24.02 ± 0.182 a
Scymnillus horni	8	3.54 ± 0.066 b	30.08 ± 0.174 a	17.84 ± 0.109 a

*** Percent = the number of scales consumed divided by the number of scales offered**
**** Numbers followed by the same letters in a column are not significantly different (*a* =0.05).**

Table 11. Predator damage location on adult female *Fiorinia externa* Ferris for five species observed during consumption studies (tested at 21º C).

Species*	Damage location** on adult female EHS***							
	Ant	Med	Post	S	W	Ant-Med	Post-Med	Ant-Post
C. pineticola	2	3	1	7	0	0	0	0
C. stigma	3	7	6	0	16	1	20	1
R. lophanthae	17	18	13	4	1	1	1	0
S. horni	9	14	11	9	3	1	5	0
S. loweii	2	0	2	4	2	0	0	0

**** C. pineticola = Conwentzia pineticola, C. stigma = Chilocorus stigma, R. lophanthae = Rhyzobius lophanthae, S. horni = Scymnillus horni, S. loweii = Scymnus loweii***
**** Ant = anterior (female scale with old second instar test), Med = medial (end of female scale, beginning of eggs), Post = posterior (eggs and exit opening for crawlers) , S = sides, W = whole, Ant-Med = anterior-medial, Post-Med = posterior-medial, Ant-Post = anterior-posterior**
***** EHS = *Fiorinia externa* Ferris or elongate hemlock scale**

Behavioral feeding response test

Scymnus loweii did not feed on any scales during the allotted test time, so it was left out of any analysis because its observed behavior was different from the other three species. For the three species analyzed, there was no significant association ($X^2 = 2.393$, df = 2, $P = 0.372$) between species for success or failure to attack EHS. There was a significant association ($X^2 = 21.876$, df = 6, $P \leq 0.002$) among the different species and recognition type they exhibited most frequently. *Chilocorus stigma* had more observations (30% for random, 0% for zigzag and circles) for a random recognition pattern than the other species. *Rhyzobius lophanthae* had the highest observations (50% for zigzag, 0% for random and circles) for the zigzag recognition pattern, and *S. horni* had the most observations (40% for circles, 30% for zigzag, 10% for random) for the circling recognition pattern.

No significant association ($X^2 = 4.821$, df = 4, $P = 0.230$) was observed between the species for a second attack on a different prey item after the first attack. For the three species, there was no significant association ($X^2 = 6.193$, df = 4, $P = 0.099$) for the attack location on EHS females. Neither was there any significant association ($X^2 = 1.698$, df = 2, $P = 0.441$) for the attack location on immatures among the different species. Each species identified the prey for different time intervals (Table 12). *Chilocorus stigma* had the shortest recognition time that was significantly lower ($F = 8.967$, df = 2, $P \leq 0.003$) than the other two species, but *R. lophanthae* and *S. horni* were not significantly different ($F = 8.967$, df = 2, $P \leq 0.003$) from each other.

From the behavioral feeding tests *S. loweii*, *R. lophanthae*, and *C. stigma* had different recognition types. *Chilocorus stigma* had the shortest prey recognition types, and *R. lophanthae* took the longest to recognize the scale as food. All species spent most of the time exploring the dish and not feeding. Consumption over longer time periods is probably a better indicator than a 30 min test because most of the species did not consume much if at all during that time period.

Table 12. Mean prey recognition time (± SD) in seconds for three coccinellid species feeding on adult female and immature *Fiorinia externa* Ferris observed during behavioral feeding response studies (tested at 21º C).

Species	Number of observations	Mean prey recognition time ± SD* (seconds)
Chilocorus stigma	**4**	**300.00 ± 213.54 b**
Rhyzobius lophanthae	**6**	**1300.00 ± 154.92 a**
Scymnillus horni	**7**	**720.00 ± 530.98 a**

*** Means followed by the same letters in a column are not significantly different (*a* =0.05).**

Feeding behavior

For the majority of the time, predators were observed to explore the Petri dish and the hemlock branch containing EHS specimens. *Rhyzobius lophanthae* quickly circled around the edges and lid of the dish at first but then moved to investigate the branch tapping its antennae while it searched for prey on the branch. For immature EHS, it flipped the first instar test up on its side and then consumed the test and nymph inside. When it was not feeding, it rested on the underside of the branch hanging upside-down or on the side of the Petri dish. *Scymnus loweii* spent most of its time moving quickly around the dish from the side of the dish to the top and down to the branch. It often rested on the underside of the branch or on the side of the Petri dish, and it circled around the dish and then moved to the branch. Once on the branch it searched for prey by tapping its antennae on the needles, zigzagging up and down a needle, and turning around in a circle at the edge of a needle. This species was active in the dish, but it was not observed feeding on EHS during the test period. *Chilocorus stigma* spent the majority of the observed time on top of the dish upside-down, and it showed little interest in the branch, but it did consume EHS during the test period.

Scymnillus horni attacked EHS more times than other species, even though 10 individuals for each species were tested. It first circled around the dish rapidly tapping its antennae, and then it moved to the branch and zigzagged or circled the needles in search of prey. It moved back and forth over the prey while tapping its antennae before consuming EHS. During one observation, it attacked an adult female scale and ate all but four eggs from inside the scale. It began by attacking the edge of the posterior end of the female scale, and it turned its head sideways while feeding and used its mandibles to chew through the center of the waxy test. It used its maxillary palps to touch the scale and to better grasp the edge of the scale while feeding, and it alternated chewing and eating eggs on the left and right sides of the scale. This allowed the species to eat all of the eggs on both sides. It pulled some of the eggs out first and then ate them. This general style of feeding was observed several times, but it sometimes began chewing on the sides or the middle of the scale. When it was not feeding, it rested on the underside of the branch where it cleaned its antennae and mandibles with its legs.

Predator competition

Predators in the different combinations had different recognition and consumption times (Table 13). For the *R. lophanthae* and *R. lophanthae* combination, they recognized the prey in less than one minute, and they also had the lowest feeding and total feeding times. The *R. lophanthae* and *S. horni* combination had a low mean recognition time (37.0 sec) and the lowest new attack time (18.0 sec), but the feeding and total feeding times were higher than for the *R. lophanthae* and *R. lophanthae* combination. The mean recognition time for predators in the *R. lophanthae*, *S. horni*, and *C. stigma* combination was higher (79.0 sec) than all other recognition times except for the *S. horni*, *R. lophanthae*, and *S. loweii* combination (175.8 sec). For the mean recognition time, the *R. lophanthae-R. lophanthae* and *R. lophanthae-S. horni* combinations were not significantly different ($F = 5.15$, df = 3, $P \leq 0.011$) from each other, but they did differ significantly from *R. lophanthae-S. horni-C. stigma* and *S. horni-R. lophanthae-S. loweiii* combinations. The two combinations with three species were not significantly different ($F = 5.15$, df = 3, $P \leq 0.011$) from each other.

The total number of attacks for each species in the different combinations tested differed depending on the species combined in the test (Table 14). The most feeding activity for all species was observed within the first day. *Rhyzobius lophanthae* individuals had the more successful attacks with all combinations except for the *R. lophanthae* and *S. horni* combination. No successful attacks on EHS occurred for *S. loweii*. *Scymnillus horni* had more successful attacks than *C. stigma*, but it had fewer attacks than *R. lophanthae*.

Competitive behavior for *R. lophanthae* pair

After both were placed in the Petri dish, they began by circling the dish until finding the branch. Moving from the branch to the side of the dish and making short flights around the dish were common behaviors. Neither individual stayed in close proximity to the other, and both would come towards each other and then move off in different directions. When both were on the branch together, the more aggressive individual would push the other along the branch with its head. Antennal contact and then

Table 13. Mean adult predator recognition and consumption time (± SD) in seconds for paired and intraguild species combinations using four coccinellids along with adult female and immature *Fiorinia externa* Ferris for competition studies (tested at 21º C).

		Mean time ± SD (seconds)			
Combination*	**N**	**Recognition**	**Feeding**	**New attack**	**Total feeding**
Rl & Rl	**12**	**37.50 ± 30.19 b**	**31.67 ± 11.93**	**18.33 ± 16.42**	**50.00 ± 22.56**
Rl & Sh	**10**	**37.00 ± 17.03 b**	**72.00 ± 42.89**	**18.00 ± 25.30**	**90.00 ± 44.72**
Rl, Sh, & Cs	**15**	**79.00 ± 73.10 a**	**88.00 ± 53.48**	**84.00 ± 98.33**	**172.00 ± 119.06**
Sh, Rl, & Sl	**12**	**175.83 ± 216.69 a**	**68.33 ± 52.54**	**26.67 ± 27.08**	**95.00 ± 51.26**

*** Rl = *Rhyzobius lophanthae*, Sh = *Scymnillus horni*, Cs = *Chilocorus stigma*, Sl = *Scymnus loweii***

**** Means followed by the same letters in a column are not significantly different (*a* =0.05).**

Table 14. Number of successful attacks on adult female and immature *Fiorinia externa* Ferris for the intraguild competition combinations by day and species using four coccinellids for competition studies (tested at 21º C).

Combination*	Day**	Species	No. successful attacks
Rl & Rl	1	Rl 1	5
		Rl 2	5
Rl & Rl	2	Rl 1	1
		Rl 2	1
Rl & Sh	1	Sh	6
		Rl	4
Rl & Sh	2	Sh	0
		Rl	0
Rl, Sh, & Cs	1	Rl	7
		Sh	3
		Cs	1
Rl, Sh, & Cs	2	Rl	1
		Sh	0
		Cs	3
Sh, Rl, & Sl	1	Sh	2
		Rl	9
		Sl	0
Sh, Rl, & Sl	2	Sh	1
		Rl	0
		Sl	0

*** Rl = *Rhyzobius lophanthae*, Sh = *Scymnillus horni*, Cs = *Chilocorus stigma*, Sl = *Scymnus loweii***

**** Day = 8 h time period where predators were observed 10 min for each h**

either moving away from each other or one pushing the other with its head occurred frequently. The encounter would begin with both touching antennae or heads together, and it ended with one moving to a different part of the dish.

Competitive behavior for *R. lophanthae* pair

After both were placed in the Petri dish, they began by circling the dish until finding the branch Moving from the branch to the side of the dish and making short flights around the dish were common behaviors. Neither individual stayed in close proximity to the other, and both would come towards each other and then move off in different directions. When both were on the branch together, the more aggressive individual would push the other along the branch with its head. Antennal contact and then either moving away from each other or one pushing the other with its head occurred frequently. The encounter would begin with both touching antennae or heads together, and it ended with one moving to a different part of the dish.

Feeding and competitive behavior for *R. lophanthae* and *S. horni* pair

Both began by circling the dish, then they moved to the branch and left the branch for the side of the dish. While *R. lophanthae* was feeding on the branch, *S. horni* avoided the branch, then it began feeding on the next needle over from *R. lophanthae*. When *S. horni* disturbed *R. lophanthae* feeding, *R. lophanthae* pushed *S. horni* with its head to stop it from feeding on the scale. Both species spent long periods of time searching that frequently resulted in no feeding. Usually neither species was on the branch at the same time or the same part of the dish because *S. horni* moved away from *R. lophanthae* when the two came near each other. Occasionally *S. horni* would bump into *R. lophanthae* with its head. While resting, *R. lophanthae* cleaned its mandibles and antennae with the tibial comb on its front tarsi.

Feeding and competitive behavior for *R. lophanthae, S. horni,* and *C. stigma*

All three species circled the dish immediately after being placed in the Petri dish, and they occasionally all searched for food on different needles without disturbances.

They all searched for prey by tapping their antennae on the branch. *Scymnillus horni* looked for leftover food under half-eaten female scales that another species had already damaged. *Chilocorus stigma* stayed on the lid of the Petri dish most of the time, or it made short flights around the dish. *Rhyzobius lophanthae* and *C. stigma* avoided each other and then came close and moved away in opposite directions. *Chilocorus stigma* chased *S. horni* away anytime it came near. *Rhyzobius lophanthae* often pushed the other two species with its head. Although *S. horni* was the smallest of the three species, it pushed the other species with its head, chased the other two species away, came up behind *R. lophanthae* and pushed it, or ran on top of *C. stigma*. *Rhyzobius lophanthae* and *C. stigma* touched antennae and then moved away in opposite directions, and *C. stigma* pushed *R. lophanthae* off the needle. *Rhyzobius lophanthae* chased *S. horni* to the underside of the needle and the end of the branch.

Feeding and competitive behavior for *R. lophanthae, S. loweii,* and *S. horni*

All three species came near each other and then moved off in opposite directions. *Scymnus loweii* came up to *S. horni* and touched the back of *S. horni* with its head, and *S. horni* moved away from *S. loweii*. *Rhyzobius lophanthae* came up to *S. loweii* and touched antennae, and *S. loweii* ran off to the other side of the branch. *Scymnus loweii* bumped into *S. horni*, and *S. loweii* moved away but *S. horni* did not move. *Scymnus loweii* avoided *R. lophanthae* while both were on the branch. *Scymnus loweii* tapped *S. horni* with its antennae and then pushed *S. horni* with its head, and *S. horni* moved away. *Scymnus loweii* made short flights around the dish.

All four of the predators tested showed aggressive tendencies, when they were tested in different combinations. The consumption for the predators was lower for the combinations than for the single species tests because of competitive behavior. If these predators had a much larger area like a tree, the aggressive behavior may not be a problem unless the predators were in high densities.

Hemlock woolly adelgid (HWA) consumption

Since HWA is the other major exotic pest on eastern hemlocks, the two most abundant EHS predators were tested to determine if HWA would be an alternate food source. For *R. lophanthae*, only 8% of female HWA with eggs were attacked and 2 to 6% of the immatures from 100 females and 150 immatures offered (Table 15). *Scymnillus horni* attacked only 4% of female HWA with eggs from the 100 offered, and it did not feed on any of the nymphs offered *Rhyzobius lophanthae* lived 9 to 14 days during the test and *S. horni* lived 12 to 16 days over the testing period.

Rhyzobius lophanthae and *S. horni* were tested to evaluate if they would eat HWA, which is a competitor of EHS on eastern hemlocks. Neither species consumed many HWA females (4-6%) or immatures (2-6%) and did not live longer than two weeks. As such, it is concluded that these predators are not good adelgid predators. Both *R. lophanthae* and *S. horni* are more specific to scales and would make better possible biological control agents for EHS than more generalist predators. *Rhyzobius lophanthae* has been successful against a variety of scales from California and other states (Gordon 1985).

Female *R. lophanthae* egg laying behavior

A total of 24 eggs was laid over the test period and most were laid singly with a couple of eggs found in pairs in different locations on the branch or Petri dish. There was one observation of three eggs laid together. Eleven eggs were laid on the vertical side of the Petri dish, and two eggs were laid on the filter paper underneath the branch. One egg was laid on the lid of the Petri dish. Eggs were laid on various parts of the branch inside the dish. On the hemlock needles, five eggs were laid on the underside and one in the middle of the top of the needle. The rest of the eggs were laid on the stem of the branch in different locations. Four eggs were laid on the attachment point of the needle to the stem. One egg was laid on the stem in between two needles, and one other egg was found lying flat and hanging off the side of the stem. The highest number of eggs laid by one female was 14. The average number of eggs laid by an individual female was 1.33. One *R. lophanthae* female was observed consuming two of its own recently laid eggs, so

Table 15. Consumption of two coccinellid species offered *Adelges tsugae* Annand as an alternate food source available on eastern hemlocks (tested at 21º C).

Species	Total no. Specimens / species	HWA Offered		HWA Eaten*			
		Female	Nymph	Female	Nymph	% Female	% Instar
Rhyzobius lophanthae	5	5	10	2	3	8.0	6.0
	5	15	20	0	2	0.0	2.0
Scymnillus horni	5	5	10	1	0	4.0	0.0
	5	15	20	0	0	0.0	0.0

*** HWA = hemlock woolly adelgid (*Adelges tsugae*)**

this species will feed on eggs of the same species. Females lay eggs almost immediately, and the first egg was observed 3 h after copulation. The number of eggs laid by a female is positively correlated ($r = 0.539$, N =17, $p = 0.026$) with the number of instars consumed. The total time females lived during the test was positively correlated ($r = 0.509$, N =17, $p = 0.037$) with the total amount of female and instar EHS eaten. Less eggs than other studies were laid overall for *R. lophanthae* (Stathas 2000a), but the low number of eggs is probably due to observed cannibalism from females eating their own eggs. The eggs were laid on many different parts of the branch and Petri dish and were most commonly laid singly.

Discussion

All six field-collected adult predators consumed adult females (0.25%-32.22%) and immatures (7.22%-37.51%) EHS, but *C. stigma*, *R. lophanthae*, and *S. horni* were more effective against EHS than the other three predators. Adult *Chilocorus stigma* consumed more adult female prey than the other species, and *R. lophanthae* consumed the most nymphs. The other four species also consumed more immatures than adult females. The first and second instar nymphs have a thinner waxy test, which makes it easier to penetrate and less time required for consumption by predators than for adult females. Larvae of *C. stigma*, *R. lophanthae*, and *S. horni* also consumed adult and immature EHS. *Chilocorus stigma* larvae consumed more adult females, and *R. lophanthae* and *S. horni* consumed more nymphs.

The predators consumed different areas or entire adult female EHS, and *R. lophanthae*, *C. stigma*, and *S. horni*, respectively, were the most aggressive of the predators with the most number of attacks of the prey source. Nymphs were completely consumed by all predators with no parts remaining. The predators attacked and began feeding on the medial, anterior or posterior (all the same amount of times), sides, and whole female scale, respectively. The attack location for *C. pineticola* was primarily on the sides, which may result in the death of the prey, but it would not affect the eggs. Predators that attacked larger sections of the adult female scale or consumed the entire

scale were able to get through the waxy test and feed on the live scale, eggs, or both *Scymnus loweii* and *C. pineticola* were less effective than the other three coccinellid predators because they attacked the sides more often and had less overall attacks.

In regard to feeding behavior, each coccinellid species had similar searching patterns for prey, and all three species tapped their antennae on the needles to pick up cues to find the EHS and recognized the prey once they had moved over it. Consumption was lower in the multiple species trials, and the four species exhibited aggressive and feeding interference behavior. Predators spent most of their time avoiding each other and not feeding. The number of successful attacks from predators progressively declined from the first to the second day, most likely as a result of predator satiation or exhaustion from predator interactions. Competition for these predators may decrease with the availability of space and less contact. Future studies using *C. stigma*, *R. lophanthae*, and *S. horni* may well demonstrate these predators are effective stabilizing agents on EHS-infested trees and qualify for augmentative releases in areas where pest suppression is needed. These three species consumed the most adult female and immature EHS as larvae and adults. *Rhyzobius lophanthae* has been a successful control agent of other diaspidid scales across the United States and Europe. Other species in the genus *Chilocorus* were effective predators of scales. The behavior and life cycle of *S. horni* should be further investigated because little is known about this species.

IV. Conclusions

Since the introduction of EHS into the eastern United States some 96 years ago, infestations have spread throughout 14 states in the eastern United States. These scales are often overlooked because of their small size, cryptic color and behavior. Over time, it has contributed to the decline and decrease in health of eastern hemlocks and sometimes mortality. The combination of this species and HWA has devastating results on the host tree causing a rapid decline in hemlock stands. While the parasitoid, *Encarsia citrina*, is believed to have entered with the EHS, no predators were documented to have entered with the initial infestation. Prior to this study, four predators of EHS (two mirids, one coniopterygid, one coccinellid) were identified in the northeastern United States (McClure 1977c, 1978a).

During this study, six established predators of EHS were collected in urban and forested sites in western North Carolina and eastern Tennessee. Two of the five coccinellid species, *S. horni* and *R. lophanthae*, represented new state records for Tennessee, and the collection of *S. loweii* denoted new county records for eastern Tennessee. *Rhyzobius lophanthae* was present as larvae and adults throughout the entire year, which makes it synchronous to the EHS life cycle.

Chilocorus stigma (native), *R. lophanthae* (introduced), and *S. horni* (native) are primarily scale predators, while *S. loweii* (introduced), *C. pineticola* (exotic), and *H. axyridis* (introduced) appeared to be generalist predators that were recorded to feed on prey other than armored scales. Both *C. stigma* and *R. lophanthae* are principally predators of species in the family Diaspididae. *Conwentzia pineticola* mainly consumes mites including spider mites, and the coccinellids, *S. loweii* and *H. axyridis*, usually consume different species of aphids. *Harmonia axyridis* will also consume mites, scales, and psyllids. *Rhyzobius lophanthae* has been successfully used as a biological control agent against a variety of diaspidid scales in the United States and at least seven other countries, and it is commercially available. Other species such as *C. kuwanae* also have been used successfully to control euonymus scale populations.

Observations showed that *Chilocorus stigma*, *R. lophanthae*, *S. horni*, and *S. loweii* all preferred to rest on the underside of the branch or needle, which kept them in close proximity to their prey. All of these species continually tapped their antennae on the needles and remained on the underside of the needles while searching for prey. *Rhyzobius lophanthae* and *C. stigma* are considered more voracious than the other predators evaluated and consumed multiple scales within a few minutes. Adult *C. stigma* consumed the most adult female EHS, and *R. lophanthae* fed upon the most immature EHS out of the six predators. The rest of the adult predators mainly consumed the immature EHS. For the larval predators, *C. stigma* consumed more adult females, while *R. lophanthae* and *S. horni* consumed more nymphs.

During competition tests, the four species were initially aggressive in their first contacts with each other, but by the second day, their aggressive behavior decreased dramatically with fewer hostile contacts. Overall, consumption during competition studies showed a decrease in comparison to the single predator consumption studies. The predators spent most of the time avoiding each other or disrupting feeding. Aggressive behavior in the field may not be an issue because increased space would decrease the possibility of encounters unless predator populations were extremely high.

The seasonal occurrence and activity of the other coccinellids varied with *C. stigma* being found most of the year, *S. horni* during the spring and summer, and *S. loweii* found primarily during the summer months. Their combined presence on an EHS-infested host could enhance the damage level that would otherwise be the case should these two species be absent. The highest numbers of predators were collected in urban than forest areas (406 and 61, respectively). All predators collected fed on EHS with three coccinellids (*C. stigma*, *R. lophanthae*, and *S. horni*, respectively) consuming the most prey.

From EHS and HWA infested trees near the sites, there was a shift in the numeric composition of the predator species present with *H. axyridis* becoming dominant and very few specimens of other predators collected. With the movement of HWA into EHS infested areas, different management strategies will need to be evaluated to protect the unique habitats formed by eastern hemlock stands. While pesticides have been effective

in urban settings, they are ineffective and expensive in forest systems. Other control strategies including the use of natural enemies may be a more effective way to protect large or dense forest areas. Mass releases of *R. lophanthae* could enhance the impact on EHS and manage the pest population. Releases of *C. stigma* or *S. horni* could also assist in controlling EHS populations. The interactions between HWA and EHS predators are not currently known but need to be evaluated for trees with both pests.

Different species of EHS predators were found in western North Carolina and eastern Tennessee than in the northeast. Predators were found throughout the year with the highest numbers in the spring and summer. The adult and larvae predators consumed EHS in laboratory studies and evidence of consumption was also present in the field. While the number of predaceous specimens collected and the percentage of field damage at less than 10% appeared low, the combination of these predators along with *E. citrina* may suppress EHS populations in forest and urban areas. This parasitoid was found to damage 17.9% to 41.3% of EHS (Lambdin et al. 2005). Together the established predators and the parasitoid may play a role in suppressing the population of EHS on eastern hemlock. *Rhyzobius lophanthae* is already mass reared, and the other coccinellid species could be reared for releases. Future studies should be done to test mass releases of different species to find the best combination.

Literature cited

Argyriou, L. C. and P. Katsoyannos. 1977. Coccinellidae species found in the olive groves of Greece. Ann. Inst. Phytopathol. Benaki (N.S.) 11: 331-345.

Baldwin, H. I. 1930. Effect of after-ripening on germination of eastern hemlock seed. J. For. 28: 853-857.

Baldwin, H. I. 1934. Further notes on the germination of hemlock seed. J. For. 32: 99-100.

Bartlett, B. and W. H. Ewart. 1951. Effect of parathion on parasitoids of *Coccus hesperidum*. J. Econ. Entomol. 44: 344-347.

Bartlett, B. and J. C. Ortega. 1952. Relation between natural enemies and DDT-induced increases in frosted scale and other pests of walnuts. J. Econ. Entomol. 45: 783-875.

Barton, L. V. 1930. Hastening the germination of some coniferous seeds. Amer. J. Bot. 17: 88-115.

Beardsley, J. W. and R. H. Gonzalez. 1975. The biology and ecology of armored scales. Annu. Rev. Entomol. 20: 47-73.

Begon, M., J. L. Haper, and C. R. Townsend 1996. Ecology, 3rd ed. Blackwell Science Ltd. Oxford, England. Biosci. 46: 401-453.

Bennett, F. D. and I. W. Hughes. 1959. Biological control of insect pests in Bermuda. Bull. Entomol. Res. 50: 423-436.

Bliss, C. I., A. W. Cressman, and B. M. Broadbent. 1935. Productivity of the camphor scale and the biology of its eggs and crawler stages. J. Agri. Res. 50: 243-266.

Bourdeau, P. F. and M. L. Laverick. 1958. Tolerance and photosynthetic adaptability to light intensity in white pine, red pine, hemlock, and ailanthus seedlings. For. Sci. 4: 196-207.

Bouvier, E. L. 1913. Coccinelles contre Cochenilles. Rev. Sci. Paris 20: 673-677.

Bray, D. F. 1958. Fiorinia hemlock scale. Sci. Tree Topics. 2: 11.

Brown, M. W. and S. S. Miller. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. Entomol. News. 109: 136-142.

Buck, S. E. 2004. Insect fauna associated with eastern hemlock, *Tsuga canadensis* (L.), in the Great Smoky Mountains National Park. M.S. Thesis, Univ. of Tennessee, Knoxville. 76 pp.

Buck, L., P. Lambdin, D. Paulsen, J. Grant, and A. Saxton. 2005. Insect species associated with eastern hemlock in the Great Smoky Mountains National Park and environs. J. Tennessee Acad. Sci. 80: 60-69.

Burgio, G., F. Santi, and S. Maini. 2002. On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Biol. Control 24: 110-116.

Burns, G. P. 1923. Studies in tolerance of New England trees. IV. Minimum light requirements referred to a definite standard Vermont Agric. Expt. Sta. Bull. 235. 32 pp.

Chapin, E. A. 1965. Coleoptera, Coccinellidae, pp. 189-254. In F. G. Werner and E. A. Chapin (eds.), Insects of Micronesia, 16. Honolulu, Hawaii: Bernice P. Bishop Museum.

Chapin, J. B., and V. A. Brou. 1991. *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). Proc. Entomol. Soc. Washington 93: 630-635.

Clausen, C. P., (ed.) 1978. Introduced parasitoids and predators of arthropod pests and weeds: A world review. U. S. Dept. Agric. Agric. Handbook 480. 545 pp.

Cock, M. J. W. 1985. A review of biological control of pests in the Commonwealth Caribbean and Bermuda up to 1982. Commonwealth Institute of Biological Control Technical Communication, Slough.

Collyer, E. 1951. The separation of *Conwentzia pineticola* End. from *Conwentzia psociformis* (Curt.), and notes on their biology. Bull. Entomol. Res. 42: 555-565.

D'Arrigo, R. D., D. M. Lawrence, E.R. Cook, W. Schuster, M. Wiljanen, and R. D. Thetford 2002. Climate-growth relationships of eastern hemlock and chestnut oak from Black Rock Forest in the Highlands of southeastern New York. Tree Ring Research.

Danoff-Burg, J. A. and S. Bird. 2002. Hemlock woolly adelgid and elongate hemlock scale: Partners in crime?, pp. 254-268. In Proceedings, Second Hemlock Woolly Adelgid Research Symposium, 5-7 February 2002, East Brunswick, New Jersey U. S. Dept. Agric., Forest Service, Forest Health Technology Enterprise Team Morgantown, West Virginia.

Daubenmire, R. F. 1931. Factors favoring the persistence of a relic association of eastern hemlock in Indiana. Butler Univ. Bot. Studies 2: 29-32.

Davidson, J. A. and C. W. McComb. 1958. Notes on the biology and control of *Fiorinia externa* Ferris. J. Econ. Entomol. 51: 405-406.

DeBach, P. 1946. An insecticidal check method for measuring the efficacy of entomophagous insects. J. Econ. Entomol. 39: 695-697.

DeBach, P. 1964. The scope of biological control, pp. 3-20. In P. DeBach (ed.), Biological control of insect pests and weeds. Reinhold Publ. Corp., New York, New York.

DeBach, P. 1974. Biological control by natural enemies. Cambridge Univ. Press, London, England. 323 pp.

DeBach, P. and D. Rosen. 1976. Armoured scale insects, pp.139-178. In V.L. Delucchi, (ed.), Studies in biological control. Cambridge Univ. Press, London, England.

DeBach, P., D. Rosen, and C.E. Kennett. 1971. Biological control of coccids by introduced natural enemies, pp. 165-194. In L.B. Huffaker (ed.), Biological control. Plenum, New York, New York.

DeBach, P. and D. Rosen. 1991. Biological control by natural enemies. Cambridge Univ. Press, London, England. 440 pp.

Deboo, R. F. and J. A. Weidhaas, Jr. 1976. Studies on the predation of pine needle scale, *Phenacaspis pinifoliae* (Fitch), by the coccinellid, *Chilocorus stigma* (Say). Can. For. Serv., Chem. Contr. Res. Inst. Report CC-X-119. Can. For. Serv., Dept. Environment, Ottawa, Canada. 23 pp.

den Boer, P. J. 1986. Facts, hypotheses and models on the part played by food in the dynamics of carabid populations, pp.81-96. In P. J. den Boer, L. Grum, and J. Szysko (eds.), Feeding behaviour and accessibility of food for carabid beetles. Warsaw Agricultural Univ. Press, Warsaw, Poland.

Denoth, M., L. Frid, and J. H. Myers. 2002. Multiple agents in biological control: improving the odds? Biol. Control 24: 20-30.

Dixon, A. F. G. 1970. Quality and availability of food for a sycamore aphid population, pp 271-287. In A. Watson, (ed.), Animal populations in relation to their food resources. Oxford Univ. Press, Edinburgh, Scotland.

Dixon, A. F. G. 1975. Seasonal changes in the fat content, form, state of gonads and length of adult life in the sycamore aphid, *Drepanosiphum plantanoides* (Schr.). Trans. Royal Entomol. Soc. London 127: 87-100.

Dobzhansky, T. 1933. Geographical variation in lady beetles. Amer. Naturalist 67: 97-126.

Doutt, R. L. 1964a. Biological characteristics of entomophagous adults, pp. 145-167. In P. DeBach (ed.), Biological control of insect pests and weeds. Reinhold Publ. Co., New York, New York.

Doutt, R. L. 1964b. The historical development of biological control, pp. 21-42. In P. DeBach (ed.), Biological control of insect pests and weeds. Reinhold Publ. Co., New York, New York.

Doutt, R. L. and P. DeBach 1964. Some biological control concepts and questions, pp. 118-142. In P. DeBach (ed.), Biological control of insect pests and weeds. Reinhold Publ. Co., New York, New York.

Drea, J. J. and R. D. Gordon. 1990. Coccinellidae, pp. 19-40. In D. Rosen (ed.), Armored scale insects, Vol 4b. Elsevier, Amsterdam, The Netherlands.

Drea, J. J. and R. M. Hendrickson. 1988. Exotic predators. Amer. Nurseryman 168: 66-71.

Ehler, L. E. 1977. Natural enemies of cabbage looper on cotton in the San Joaquin valley. Hilgardia 45: 73-106.

El-Sebaey, I. I. A. and A. M. El-Gantiry. 1999. Biological aspects and description of different stages of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). Bull. Faculty Agric., Cairo Univ. 50: 87-97.

Enderlein, G. 1905. *Conwentzia pineticola* nov. gen., nov. spec., eine neue Neuroptera aus Westpreussen. Ber. westpreuss. Bot.-zool. Ver. 26-27: 10-12. (translated by Elsie Collyer)

Enderlein, G. 1907. Nachtrage zur Monographie der Coniopterygiden. Stettin. Entomol. Ztg. 68: 10-13. (translated by Elsie Collyer)

Endler, J. A. 1991. Interactions between predators and prey, pp. 169-196. In J. R. Krebs and N. B. Davies (eds.), Behavioral ecology, 3rd ed. Blackwell Sci. Publ., Oxford, England.

Eyre, F. H. and W. M. Zillgitt. 1953. Partial cuttings in northern hardwoods of the Lake States. U. S. Dept. Agric.Tech. Bull. 1076. 124 pp.

Ferris, G. F. 1936. Contributions to our knowledge of the Coccoidae (Hemiptera). Microentomol. 1: 1-16.

Ferris, G. F. 1942. Atlas of the scale insects of North America. Standford Univ. Press, California. Series 4: 393.

Finzi, A. C., C. D. Canham, and N. Van Breemen. 1998. Canopy tree-soil interactions within temperate forests: Species effects on pH and cations. Ecol. Applic. 8: 447-454.

Fowells, H. A. 1965. Silvics of forest trees of the United States. U. S. Dept. of Agric., For. Serv., Div. Timber Management, Agric. Handbook 271. Washington, DC. 762 pp.

Friesner, R. C. and J. E. Potzger. 1932. Studies in forest ecology. I. Some factors concerned in hemlock reproduction in Indiana. II. The ecological significance of *Tsuga canadensis* in Indiana. Butler Univ. Bot. Studies 2: 133-149.

Friesner, R. C. and J. E. Potzger. 1934. Climax conditions and ecological status of *Pinus strobes*, *Taxus canadensis*, and *Tsuga canadensis* in the Pine Hills region of Indiana. Butler Univ. Bot. Studies 3: 65-83.

Friesner, R. C. and J. E. Potzger. 1936. Soil moisture and the nature of the *Tsuga* and *Tsuga-Pinus* forest associations in Indiana. Butler Univ. Bot. Studies 3: 207-209.

Friesner, R. C. and J. E. Potzger. 1944. Survival of hemlock seedlings in a relict colony under forest conditions. Butler Univ. Bot. Studies 6: 102-115.

Frothingham, E. H. 1915. The eastern hemlock. U. S. Dept Agric. Bull. 152. 43 pp.

Fuller, J. L. 1998. Ecological impact of the mid-Holocene hemlock decline in Southern Ontario, Canada. Ecol. 79: 2337-2351.

Garrett, W. T. and G. S. Langford 1969. Control of *Fiorinia externa* on hemlock in Maryland J. Econ. Entomol. 62: 1449-1450.

Gentile, A. G. and F. M. Summers. 1958. The biology of the San Jose scale on peaches with special reference to the behavior of males and juveniles. Hilgardia 27: 269-285.

Goder, H. A. 1956. A phytosociological study of *Tsuga canadensis* near the termination of its range in Wisconsin. Wisconsin Univ. Dissert. Abs. 16: 438.

Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America North of Mexico. J. New York Entomol. Soc. 93: 1-912.

Graham, S. A. 1941a. Climax forests of the Upper Pennisula of Michigan. Ecol. 22: 355-362.

Graham, S. A. 1941b. The question of hemlock establishment. J. For. 39: 567-569.

Graham, S. A. 1943. Causes of hemlock mortality in northern Michigan. Mich Univ. School For. Conserv. Bull. 10. 62 pp.

Grasovsky, A. Y. 1929. Some aspects of light in the forest. Yale Univ. School For. Bull. 23. 53 pp.

Greathead, D. J. and R. D. Pope. 1977. Studies on the biology and taxonomy of some *Chilocorus* spp. (Coleoptera: Coccinellidae) preying on *Aulacaspis* spp. (Hemiptera: Diaspididae) in East Africa, with the descriptions of a new species. Bull. Entomol. Res. 67: 259-270.

Hagen, K. S. 1987. Nutritional ecology of terrestrial insect predators, pp. 533-577. In F. Slansky Jr., F. and J. G. Rodriquez (eds.), Nutritional ecology of insects, mites, spiders, and related invertebrates. John Wiley & Sons, New York, New York.

Hagen, K. S., S. Bombosch, and J. A. McMurtry. 1976. The biology and impact of predators, pp. 93-142. In C. B. Huffaker and P. S. Messenger (eds.), Theory and practice of biological control. Academic Press, New York, New York.

Hassell, M. P. and R. M. May. 1986. Generalist and specialist natural enemies in insect predator-prey interactions. J. Anim. Ecol. 55: 923-940.

He, J. L., E. P. Ma, Y. C. Shen, W. L. Chen, and X. Q. Sun. 1994. Observations of the biological characteristics of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). J. Shanghai Agric. College 12: 119-124.

Hironori, Y. and S. Katsuhiro. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga 42: 153-163.

Hodek, I. 1973. Life history and biological properties, pp.70-76. In I. Hodek (ed.), Biology of Coccinellidae. Dr. W. Junk N. V., Publishers, The Hauge, Holland.

Hodek, I. 1993. Habitat and food specificity in aphidophagous predators. Biocontrol Sci. Tech. 3: 91-100.

Hodek I. 1996. Food relationships. In I. Hodek and A. Honek (eds.), Ecology of Coccinellidae. Kluwer Acad. Publ., Dordrecht, The Netherlands.

Honek, A. 1996. Variability and genetic studies In: I. Hodek and A. Honek (eds.), Ecology of Coccinellidae. Kluwer Academic Publ., Dordrecht, The Netherlands.

Hough, A. F. 1936a. A climax forest community on East Tionesta Creek in northwestern Pennslyvania. Ecol. 17: 9-28.

Hough, A. F. 1936b. The dying of hemlock and other species on the Allegheny National Forest. U. S. For. Serv. Allegheny Northeast For. Expt. Sta. Tech. Note 7. 2 pp.

Hough, A. F. 1942. Soils in a virgin hemlock-beech forest on the northern Allegheny Plateau. Soil Sci. 54: 335-341.

Hough, A. F. 1943. Soil factors and stand history in a virgin forest valley on the northern Allegheny Plateau. Soil Sci. 56: 19-28.

Hough, A. F. 1945. Frost pocket and other microclimates in forests of the northern Allegheny Plateau. Ecol. 26: 235-250.

Hough, A. F. and R. D. Forbes. 1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. Ecol. Monog. 13: 299-320.

Hoy, M. A. 1994. Parasitoids and predators in management of arthropod pests, pp. 129-198. In R. L. Metcalf and W. H. Luckmann (eds.), Introduction to insect pest management, 3rd ed. John Wiley & Sons, New York, New York.

Hu, Y. S., Z. M. Wang, C. L. Ning, Z. Q. Pi, and G. Q. Gao. 1989. The functional response of *Harmonia* (*Leis*) *axyridis* to their prey of *Cinara* sp. Natural Enemies of Insects 11: 164-168.

Hukusima, S and M. Kamei. 1970. Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Research Bull. Faculty Agric., Gifu Univ. 29: 53-66.

Huston, M. A. 1994. Biological diversity: The coexistence of species on changing landscapes. Cambridge Univ. Press, Cambridge, United Kingdom. 681 pp.

Jenkins, J. C., J. D Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Can. J. For. Res. 29: 630-645.

Jennings, O. E. 1927. Classification of the plant societies of central and western Pennsylvania. Pennsylvania Acad Sci. Proc. 1: 23-55.

Johnson, W. T. and H. H. Lyon. 1976. Insects that feed on trees and shrubs: An illustrated practical guide. Cornell Univ. Press, Ithaca, NY. 464 pp.

Kalaskar, A. and E. W. Evans. 2001. Larval responses of aphidophagous lady beetles (Coleoptera: Coccinellidae) to weevil larvae versus aphids as prey. Ann. Entomol. Soc. Amer. 94: 76-81.

Katsoyannos, P. 1996. Integrated insect pest management for citrus in Northern Mediterranean countries. Benaki Phytopathological Institute, Kifissia, Athens, Greece. 110 pp.

Katsoyannos, P., D. C. Kontodimas, G. J. Stathas, C. T. Tsartsalis. 1997. Establishment of *Harmonia axyridis* on citrus and some data on its phenology in Greece. Phytoparasitica. 25: 183-191.

Kawauchi, S. 1979. Effects of temperatures on the aphidophagous Coccinellids. Kurume Univ. J. 28: 47-52.

Kidd, K. A., C. A. Nalepa, E. R. Day, and M. G. Waldvogel. 1995. Distribution of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in North Carolina and Virginia. Proc. Entomol. Soc. Washington 97: 729-731.

Koch, R. L. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. J. Insect Sci. 3: 32. insectscience.org/3:32.

Koch, R. L. and W. D. Hutchison. 2003. Phenology and blacklight trapping of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Minnesota agricultural landscape. J. Entomol. Sci. 38: 477-480.

Koch, R. L., W. D. Hutchison, R. C. Venette, and G. E. Heimpel. 2003. Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). Biol. Control 28: 265-270.

Korschefsky, R. 1932. Coccinellidae, pp. 439-447. In S. Schenkling (ed.), Coleopterorum Catalogus. Berlin.

Kosztarab, M. 1996. Scale insects of northeastern North America. Virginia Mus. Natural Hist. Special Publication No. 3, Martinsville, VA. 415 pp.

Kuznetsov, V. N. 1997. Lady beetles of Russian Far East: Memoir series of the center for systematic entomology, number 1. Saint Lucie Pr, Gainesville, FL.

LaForest, J. 2000. Diversity and distribution of the insect fauna associated with tulip-poplar in east Tennessee. M.S. Thesis, Univ. of Tennessee, Knoxville. 21-50 pp.

LaMana, M. L. and J. C. Miller. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Bio. Control 6: 232-237.

LaMana, M. L. and J. C. Miller. 1998. Temperature-dependent development in an Oregon population of *Harmonia axyridis* (Coleoptera: Coccinellidae). Environ. Entomol. 27: 1001-1005.

Lambdin, P.L. 1995. Release, development and establishment of *Chilocorus kuwanae* Silvestri for control of *Unaspis euonymi* (Comstock) in Tennessee. Israel J. Entomol. 19: 327-330.

Lambdin, P.L., C. Lynch, J. F. Grant, R. Reardon, B. Onken, and R. Rhea. 2005. Elongate hemlock scale and its natural enemies in the Southern Appalachians, pp. 145-154. In B. Onken and R. Reardon (eds.), Proc. Third symposium on hemlock woolly adelgid in the eastern United States, 1-3 February 2005, Asheville, North Carolina. U. S. Dept. Agric., For. Serv., Morgantown, West Virginia.

Lapin, B. 1994. The impact of hemlock woolly adelgid on resources in the Lower Connecticut River Valley. Report for the NE Center for Forest Health Research Hamden, Connecticut: U. S. Dept. Agric., For. Serv. 45 pp.

Listo, J., E. M. Listo, and V. Kanervo. 1939. Tutkimuksia hedelmapuupunkista (*Paratetranychus pilosus* C. & F.) Valt. Maatalousk. Julk., no. 99, 143 pp. (translated by Elsie Collyer)

Liu, H and L. Qin. 1989. The population fluctuations of some dominant species of ladybird beetles in Eastern Hebei Province. Chinese J. Biol. Control 5: 92.

Lou, H. H. 1987. Functional response of *Harmonia axyridis* to the density of *Rhopalosiphum prunifoiae*. Natural Enemies of Insects. 9: 84-87.

Lord, F. T. 1947. The influence of spray programs on the fauna of apple orchards in Nova Scotia: II Oystershell scale, *Lepidosaphes ulmi* (L.). Can. Entomol. 79: 196-209.

Lucas, E., D. Coderre, and C. Vincent. 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. Entomol. Exper. et Appl. 85: 151-159.

Lutz, H. J. 1928. Trends and silvicultural significance of upland forest successions in southern New England Yale Univ. School For. Bull. 22. 68 pp.

Lutz, H. J. 1930. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. Ecol. 9: 1-29.

Mahr, S. 1996. Know your friends: multicolored Asian lady beetle. Midwest Biol. Control News, Online. (http://www.entomology.wisc.edu/mbcn/kyf210.html) 2.

Maissurow, D. K. 1935. Fire as a necessary factor in the perpetuation of white pine. J. For. 33: 373-378.

Marshall, R. 1927. The growth of hemlock before and after release from suppression. Harvard For. Bull. 41. 41 pp.

Martin, N. D. 1959. An analysis of forest succession in Algonquin Park, Ontario. Ecol. Monog. 29: 187-218.

Matadha, D., G. C. Hamilton, M. G. Hughes, and J. H. Lashomb. 2003. Distribution of natural enemies of Euonymus scale, *Unaspis euonymi* (Comstock) (Homoptera: Diaspididae), in New Jersey. Eviron. Entomol. 32: 602-607.

Mattson, W. J. and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. Sci. 190: 515-522.

Mayer, M. and D. C. Allen. 1983. *Chilocorus stigma* (Coleoptera: Coccinellidae) and other predators of beech scale in central New York, pp. 89-98. In D. R. Houston and D. Wainhouse (eds.), Proc. IUFRO beech bark disease working party conference, 26 September to 8 October 1982, Hamden, Connecticut. U. S. Dept. Agric., For. Serv., Northeastern For. Exper. Station, Newtown Square, Pennsylvania.

McClure, M. S. 1976. Colonization and establishment of the red pine scale, *Matsucoccus resinosae* B&G (Hemiptera: Margarodidae), in a Connecticut plantation. Environ. Entomol. 5: 943-947.

McClure, M. S. 1977a. Population dynamics of the red pine scale, *Matsucoccus resinosae* (Hemiptera: Margarodidae): the influence of resinosis. Environ. Entomol. 6: 789-795.

McClure, M. S. 1977b. Dispersal of the scale *Fiorinia externa* (Hemiptera: Diaspididae) and effects of edaphic factors on its establishment on hemlock. Environ. Entomol. 6: 539-544.

McClure, M. S. 1977c. Resurgence of the scale, *Fiorinia externa* (Hemiptera: Diaspididae), on hemlock following insecticide application. Environ. Entomol. 6: 480-484.

McClure, M. S. 1977d. Parasitism of the scale insect, *Fiorinia externa* (Hemiptera: Diaspididae), by *Encarsia citrina* (Hymenoptera: Eulophidae) in a hemlock forest: Density dependence. Environ. Entomol. 6: 551-555

McClure, M. S. 1978a. Two parasitic wasps have potential for controlling hemlock scales. Front. Plant Sci. 30: 2-3.

McClure, M. S. 1978b. Seasonal development of *Fiorinia externa*, *Tsugaspidiotus tsugae* (Hemiptera: Diaspididae), and their parasitoid *Encarsia citrina* (Hymenoptera: Aphelinidae): importance of parasitoid-host synchronism to the population dynamics of two scale pests of hemlock. Environ. Entomol. 7: 863-870.

McClure, M. S. 1978c. Effectiveness of foliar systemic insecticides for controlling scales on forest and ornamental hemlock. Entomol. Soc. Amer., Insecticide and Acaricide Tests 3: 146-147.

McClure, M. S. 1979a. Self-regulation in populations of the elongate hemlock scale, *Fiorinia externa* (Hemiptera: Diaspididae). Oecologia. 39: 25-36.

McClure, M. S. 1979b. Spatial and seasonal distribution of disseminating stages of *Fiorinia externa* (Homoptera: Diaspididae) and natural enemies in a hemlock forest. Environ. Entomol. 8: 869-873.

McClure, M. S. 1980a. Foliar nitrogen: A basis for host suitability for the elongate hemlock scale, *Fiorinia externa* (Hemiptera: Diaspididae). Ecol. 61: 72-79.

McClure, M. S. 1980b. Competition between exotic species: Scale insects on hemlock. Ecol. 61: 1391-1401.

McClure, M. S. 1981a. Effects of voltinism, interspecific competition and parasitism on the population dynamics of the hemlock scales, *Fiorinia externa* and *Tsugaspidiotus tsugae* (Hemiptera: Diaspididae). Ecol. Entomol. 6: 47-54.

McClure, M. S. 1981b. Self-regulation in populations of the elongate hemlock scale, *Fiorinia externa* (Hemiptera: Diaspididae): Role of food quantity and quality. Misc. Publ. Entomol. Soc. Amer. 11: 33-40.

McClure, M. S. 1983a. Competition between herbivores and increased resource heterogeneity, pp 125-153. In R. F. Denno and M. S. McClure (eds.), Variable plants and herbivores in natural and managed systems. Acad. Press, New York, New York.

McClure, M. S. 1983b. Population dynamics of a pernicious parasitoid: Density-dependent vitality of red pine scale. Ecol. 64: 710-718.

McClure, M. S. 1983c. Reproduction and adaptation of exotic hemlock scales (Hemiptera: Diaspididae) on their new and native hosts. Environ. Entomol. 12: 811-815.

McClure, M. S. 1986a. Population dynamics of Japanese hemlock scales: A comparison of endemic and exotic communities. Ecol. 67: 1411-1421.

McClure, M. S. 1986b. Role of predators in regulation of endemic populations of *Matsucoccus matsumarae* (Homoptera: Margarodidae) in Japan. Environ. Entomol. 15: 976-983.

McClure, M. S. 1987. Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* Bean and Godwin (Homoptera: Margarodidae) in the United States. Environ. Entomol. 16: 224-230.

McClure, M. S. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae). Ann. Entomol. Soc. Amer. 8: 50-54.

McClure, M. S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Hemiptera: Adelgidae) on *Tsuga canadensis*. Environ. Entomol. 20: 258-264.

McClure, M. S. 1995. Using natural enemies to control hemlock woolly adelgid Front. Plant Sci. 47: 2.

McClure, M. S. 1996. Biology of *Adelges tsugae* and its potential for spread in the Northeastern United States, pp 16-23. In Salom, S. M., T. C. Tigner, and R. C. Reardon (eds.), *In* Proc. The First Hemlock Woolly Adelgid Review, 12 October 1995, Charlottesville, Virginia. U. S. Dept. Agric., For. Serv., Morgantown, West Virginia.

McClure, M. S. 2002a. The elongate hemlock scale, *Fiorinia externa* Ferris (Hemiptera: Diaspididae): A new look at an old nemesis, pp. 248-253. In B. Onken, R. Reardon, and J. Lashomb (eds.), Proc. Hemlock Woolly Adelgid in the Eastern United States Symposium, 5-7 February 2002, East Brunswick, New Jersey. New Jersey Agric. Exper. Station and Rutgers Univ.

McClure, M. S. 2002b. Elongate hemlock scale. Pest Alert Leaflet NA-PR-01-02. U. S. Dept. of Agric., For. Serv., Northeastern Area, Morgantown, WV. 2 pp.

McClure, M. S. and C. A. S-J Cheah 1999. Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), in eastern North America. Biol. Invasions. 1: 241-254.

McClure, M. S., S. M. Salom, and K. S. Shields. 2001. Hemlock Woolly Adelgid. FHTET 2001-03. U.S. Dept. of Agric., For. Serv., For.Health Technology Enterprises Team, Morgantown, West Virginia. 14 pp.

McComb, C. W. and J. A. Davidson. 1960. The hemlock scale, *Fiorinia externa* Ferris, a scale pest of hemlock. Univ. Maryland, Entomol. Leafl. 17. 2 pp.

McIntyre, A. C. and L. G. Schnur. 1936. Effects of drought on oak forests. Pennsylvania State Col. Agric. Expt. Sta. Bull. 325. 43 pp.

McNeill, S. and T. R. E. Southwood 1978. The role of nitrogen in the development of insect plant relationships, pp 77-98. In J. B. Harborne (ed.), Biochemical aspects of plant and animal coevolution. Proc., Phytochemical Soc. Europe 15. Acad. Press, London, England.

Mendel, Z., F. Assael, S. Zeidan, and A. Zehavi. 1998. Classical biological control of *Palaeococcus fuscipennis* (Burmeister) (Homoptera: Margarodidae) in Israel. Biol. Control. 12: 151-157.

Merrill, P. H and R. C. Hawley. 1924. Hemlock: Its place in the silviculture of the southern New England forest. Yale Univ. School For. Bull. 12.

Michaud, J. P. 2001. Numerical response of Olla V-Nigrum (Coleoptera: Coccinellidae) to infestations of Asian Citrus Psyllid, (Hemiptera: Psyllidae) in Florida. Florida Entomol. 84: 608-612.

Michaud, J. P. 2002. Biological control of Asian citrus psyllid, *Diaphorina citri* (Hemiptera: Psyllidae), in Florida: A preliminary report. Entomol. News. 113: 216-222.

Michaud, J. P. 2003. A comparative study of larval cannibalism in three species of ladybird Ecol. Entomol. 28: 92-101.

Miles, M. L. and E. C. Smith 1960. A study of the origin of hemlock forests in southwestern Nova Scotia. For. Chron. 36: 375-390.

Miller, D. R. and M. Kosztarab. 1979. Recent advances in the study of scale insects. Annu. Rev. Entomol. 24: 1-27.

Miller, D. R. and J. A. Davidson. 2005. Armored scale insect pests of trees and shrubs (Hemiptera: Diaspididae). Comstock Publishing Associates, Cornell Univ. Press, Ithaca, New York. 442 pp.

Mitchell, J. M. 1999. Habitat relationships of five northern bird species breeding in hemlock ravines in Ohio, USA. Natural Areas J. 19: 3-11.

Moore, B., H. M. Richards, H. A. Gleason, and A. B. Stout. 1924. Hemlock and its environment. I. Field records. New York Bot. Gard Bull. 12: 325-350.

Morey, H. F. 1936. Age-size relationship of Hearts Content, virgin forest in northwestern Pennsylvania. Ecol. 17: 251-257.

Muma, M. H. 1955. Some ecological studies on the twice-stabbed lady beetle *Chilocorus stigma* (Say). Ann. Entomol. Soc. Amer. 48: 493-498.

Musser, F. R. and A. M. Shelton. 2003. Bt sweet corn and selective insecticides: Impacts on pests and predators. J. Econ. Entomol. 96: 71-80.

Nalepa, C. A. 1992. Pollen and nectar feeding by *Chilocorus kuwanae* (Silvestri) (Coleoptera: Coccinellidae). Proc. Entomol. Soc. Washington. 94: 596-597.

Nilsson, P. A. 2001. Predator behavior and prey density: Evaluating density-dependent intraspecific interactions on predator functional responses. J. Anim. Ecol. 70: 14-19.

Obata, S. 1986. Determination of hibernation site in the ladybird beetle, *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). Kontyu. 54: 218-223.

Obrycki, J. J., M. J. and C. A. Tauber, and J. R. Ruberson. 2006. Prey specialization in insect predators. In E. B. Radcliffe and W. D. Hutchison (eds.), Radcliffe's IPM world textbook, URL http: impworldumn.edu, Univer. Minnesota, St. Paul, Minnesota.

Olkowski, W., E. Dietrick, and H. Olkowski. 1992. The biological control industry in the United States, part 3. IPM Practitioner. 14: 1-18.

Olson, J. S. 1954. Germination and survival of eastern hemlock seedlings in Connecticut seedbeds. Ecol. Soc. Amer. Bull. 35: 60.

Olson, J. S., F. W. Stearns, and H. Nienstaedt. 1959. Eastern hemlock seeds and seedlings' response to photoperiod and temperature. Connecticut Agric. Expt. Sta. Bull. 620. 70 pp.

Ongagna, P., L. Giuge, G. Iperti, and A. Ferran. 1993. Cycle de development d' *Harmonia axyridis* (Col. Coccinellidae) dans son aire d' introduction: le sud-est de la France. Entomophaga. 38: 125-128. (translated by R. Koch)

Oosting, H. J. and D. W. Hess. 1956. Microclimate and relict stand of *Tsuga canadensis* in the lower Piedmont of North Carolina. Ecol. 37: 28-39.

Orwig, D. A. and D. R. Foster. 1996. Forest ecosystem response to hemlock woolly adelgid outbreak in southern New England Bull. Ecol. Soc. Amer. 77: 335.

Orwig, D. A. and D. R. Foster. 1998. Forest response to introduced hemlock woolly adelgid in southern New England, USA. J. Torrey Botanical Soc. 125: 60-73.

Osawa, N. 1989. Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. Researches Pop. Ecol. 31: 153-160.

Osawa, N. 1993. Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life tables and key factor analysis. Researches on Pop. Ecol. 35: 335-348.

Osawa, N. 2000. Population field studies on the aphidophagus ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. Population Ecol. 42: 115-127.

Parker, B. L., M. Skinner, S. Gouli, T. Ashikaga, and H. B. Teillon. 1998. Survival of hemlock woolly adelgid (Hemiptera: Adelgidae) at low temperatures. For. Sci. 44: 414-420.

Percival, W. S. 1933. A contribution to the biology of *Fomes pini* (Thore) Lloyd (*Trametes pini*) (Thore) (Fries). New York State Col. For. Tech Pub. 40. 72 pp.

Prasifka, J. R., K. M. Heinz, and C. G. Sansone. 2004. Timing, magnitude, rates, and putative causes of predator movement between cotton and grain sorghum fields. Environ. Entomol. 33: 282-290.

Price, P. W. 1975. Insect ecology. John Wiley and Sons, New York, New York. 514 pp.

Price, P. W. 1984. Insect ecology, 2nd ed. John Wiley and Sons, New York, New York. 211 pp.

Price, P. W. and G. P. Waldbauer. 1994. Ecological aspects of pest management, pp. 35-72. In R. L. Metcalf and W. H. Luckmann (eds.), Introduction to insect pest management, 3rd ed. John Wiley and Sons, New York, New York.

Ripper, W. E. 1956. Effect of pesticides on balance of arthropod populations. Annu. Rev. Entomol. 1: 403-438.

Rodriquez, J. G. 1960. Nutrition of the host and reaction to pests, pp. 149-167. In L. P. Reitz (ed.), Biological and chemical control of plants and animal pests, Amer. Assoc. Adv. Sci. Publ. No. 61, Washington, D C.

Rosen, D. 1990. Amored scale insects: Their biology, natural enemies and control. Elsevier, Amsterdam, Vol. 4B. 688 pp.

Rosen, D. and P. DeBach 1978. Diaspididae, pp. 78-128. In C. P. Clausen (ed.), Introduced parasites and predators of arthropod pests and weeds: a world review. U. S. Dept. Agric., Washington, D C.

Royle, D. D. and R. G. Lathrop. 1997. Monitoring hemlock forest health in New Jersey using Landsat TM data and change direction techniques. For. Sci. 43: 327-335.

Rubstov, I. A. 1952. *Lindorus* – an effective predator of diapsine scales. Entomol. Obozr. 32: 96-106.

Rungs, C. 1950. Sur l'extension spontanee au Maroc du *Rhyzobius* (*Lindorus*) *lophanthae* Blaisdell (Col.: Coccinellidae). Bull. Soc. Entomol. Fr. 55: 9-11. (translated by G. Stathas)

Sabelis, M. W. 1992. Predatory arthropods, pp. 225-264. In M. J. Crawley (ed.), Natural enemies. Blackwell Scientific Pubs., Oxford, England.

Sakurai, H., T. Kawai, and S. Takeda. 1992. Physiological changes related to diapause of the lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Applied Entomol. and Zool. 27: 479-487.

Sakurai, H., Y. Kumada, and S. Takeda. 1993. Seasonal prevalence and hibernating-diapause of the lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Applied Entomol. and Zool. 27: 479-487.

Salvadores, A. Z. 1913. El Duranzo (The Peach). Reprint from Bol. Minist. Agri. Buenos Aires (in Rev. Appl. Entomol. 1914) II.

Samways, M. J., R. Osborn, H. Hastings, and V. Hattingh1999. Global climate change and accuracy of prediction of species' geographical ranges: establishment success of introduced ladybirds (Coccinellidae, *Chilocorus* spp.) worldwide. J. Biogeography 26: 795-812.

Sasaji, H. 1971. Fauna Japonica, Coccinellidae (Insecta: Coleoptera). Tokyo: Academic Press, Japan. 340 pp.

Sasaji, H. 1977. Larval characters of Asian Species of the Genus *Harmonia* Mulsant. Memoir Faculty Education Fukui Univer. Series II Nat. Sci. 27: 1-17

Sasscer, E. R. 1912. The genus *Fiorinia* in the United States. U. S. Dept. Agric.,Bur. Entomol. Tech. Serv. 16: 75-82.

Savoiskaya, G. I. 1970a. Coccinellids of the Alma-Ata reserve. Trudy Alma Atinskogo Gosudarstvennogo Zapovednika. 9: 163-187.

Savoiskaya, G. I. 1970b. Introduction and acclimatisation of some coccinellids in the Alma-Ata reserve. Trudy Alma Atinskogo Gosudarstvennogo Zapovednika 9: 138-162.

Savoiskaya, G. I. and B. Klausnitzer. 1973. Morphology and taxonomy of the larvae with keys for their identification, pp.36-55. In I. Hodek (ed.), Biology of Coccinellidae. Dr. W. Junk N. V., Publishers, The Hauge, Holland.

Schweig, C. and A. Grunberg. 1936. The problem of the black scale, *Chrysomphalus ficus* (Ashm.), in Palestine. Bull. Entomol. Res. 27: 677-714.

Secrest, H. C., H. J. MacAloney, and R. C. Lorenz. 1941. Causes of the decadence of hemlock at the Menominee Indian Reservation, Wisconsin. J. For. 39: 3-12.

Settle, W. H., H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, and A. S. Lestari. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecol. 77: 1975-1988.

Shreve, F. 1927. Soil temperatures in redwood and hemlock forests. Torrey Bot. Club Bull. 54: 649-656.

Shreve, F., M. A. Chrysler, F. H. Blodgett, and F. W. Besley. 1910. The plant life of Maryland. Maryland Weather Serv. Spec. Pub. 3. 533 pp.

Shu, C. R. and C. Y. Yu. 1985. An investigation on the natural enemies of *Hyphantria cunea*. Natural Enemies of Insects. 7: 91-94.

Sih, A. 1987. Predators and prey lifestyles: An evolutionary and ecological overview, pp. 203-224. In W. C. Kerfoot and A. Sih (eds.), Predation. Univer. Press of New England, Hanover, New Hampshire.

Smirnoff, W. 1950. Sur la biologie au Maroc de *Rhyzobius* (*Lindorus*) *lophanthae* Blaisdell (Col.: Coccinellidae). Rev. Pathol. Veg. Entomol. Agric. Fr. 29: 190-194. (translated by G. Stathas)

Snyder, W. E., S. N. Ballard, S. Yang, G. M. Clevenger, T. D. Miller, J. J. Ahn, T. D. Hatten, and A. A. Berryman. 2004. Complementary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoid *Aphelinus asychis* on greenhouse roses. Biol. Control. 30: 229-235.

Soares, A. O., D. Coderre, and H. Schanderl. 2001. Fitness of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). European J. Entomol. 98: 287-293.

Southwood, T. R. E. 1973. The insect/plant relationship-an evolutionary perspective, pp. 3-30. In H. F. van Emden (ed.), Symposia of the Royal Entomological Society of London, Insect/plant relationships, vol. 6. John Wiley and Sons, New York, New York.

Souto, D., T. Luther, and B. Chianese. 1996. Past and current status of hemlock woolly adelgid in eastern and Carolina hemlock stands, pp. 9-15. In Salom, S.M., T.C. Tignor, and R.C. Reardon (eds.), Proc. First Hemlock Woolly Adelgid Review, 12 October 1995, Charlottesville, Virginia. U. S. Dept. Agric., Forest Service, Morgantown, West Virginia.

Stange, L. A. 2000. A preliminary list of Neuroptera from the Great Smoky Mountains National Park. Insecta Mundi. 14: 232.

Stark, R. W. 1965. Recent trends in forest entomology. Annu. Rev. Entomol. 10: 303-324.

Stathas, G. J. 2000a. The effect of temperature on the development of the predator *Rhyzobius lophanthae* and its phenology in Greece. Biocontrol. 45: 439-451.

Stathas, G. J. 2000b. *Rhyzobius lophanthae* prey consumption and fecundity. Phytoparasitica. 28: 3.

Stearns, F. and J. Olson. 1958. Interaction of photoperiod and temperature affecting seed germination in *Tsuga canadensis*. Amer. J. Bot. 45: 53-58.

Stelzl, M. and D. Devetak. 1999. Neuroptera in agricultural ecosystems. Agric., Ecosystems and Environ. 74: 305–321

Stickel, P. W. 1933. Drought injury in hemlock-hardwood stands in Connecticut. J. For. 31: 573-577.

Stoeckeler, J. H. and C. Arbogast, Jr. 1955. Forest management lessons from a 1949 windstorm in northern Wisconsin and upper Michigan. U. S. For. Serv. Lake States For. Exper. Sta., Sta. Paper 34. 11 pp.

Stuart, R. J., J. P. Michaud, L. Olsen, and C. W. McCoy. 2002. Lady beetles as potential predators of the root weevil *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in Florida citrus. Florida Entomol. 85: 409-416.

Sunderland, K. D. 2001. Invertebrate pest control by carabids, pp.165-214. In J. M. Holland (ed.), The agroecology of carabid beetles. Intercept, Andover, UK.

Sunderland, K. D., J. A. Axelsen, K. Dromph, B. Freier, J. L. Hempinne, N. H. Holst, P.J. M. Mols, M. K. Petersen,W. Powell, P. Ruggle, H. Triltsch, and L. Winder. 1997. Pest control by a community of natural enemies. Acta Jutlandica. 72: 271-326.

Symondson, W.O.C., K. D. Sunderland, and M. H. Greenstone. 2002. Can generalist predators be effective biocontrol agents? Annu. Rev. Entomol. 47: 561–594.

Takagi, S. 1963. *Fiorinia externa* and *Tsuga sieboldii* in Japan. Insecta Matsumurana. 26: 115-117.

Takahashi, K. 1987. Differences in oviposition initiation and sites of lady beetle, *Coccinella septempunctata bruckii* Mulsant and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in the field. Japanese J. Applied Entomol. Zool. 31: 253-254.

Takahashi, R. and S. Takagi. 1957. A new genus of Diaspididae from Japan (Cocciodea, Hemiptera). Kontyu. 25: 102-105.

Talerico, R. L., C. W. McComb, and W. T. Garrett. 1967. *Fiorinia externa* Ferris, a scale insect of hemlock, U.S. Dept. of Agric. Forest Pest Leaflet 107. 4 pp.

Tanagishi, K. 1976. Hibernation of the lady beetle, *Harmonia axyridis*. Insectarium. 13: 294-298.

Tedders, W. L. and P. W. Schaefer. 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. Entomol. News. 105: 228-243.

Thompson, W. R. 1929. On the relative value of parasitoids and predators in the biological control of insect pests. Bull. Entomol. Res. 19: 343-350.

Thompson, W. L. 1939. Cultural practices and their influences on citrus pests. J. Econ. Entomol. 32: 782-789.

Thompson, J. R. and F. J. Simmonds. 1965. A catalogue of the parasites and predators of insect pests, Section IV. Host-predator catalogue. Commonwealth Agric. Bureau, Commonwealth Inst. Biol. Control, Ottawa, Ontario. 198 pp.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geog. Rev. 38: 55-94.

Trieff, D. 2002. Composition of the Coleoptera and associated insects collected by canopy fogging of northern red oak (*Quercus rubra* L.) trees in the Great Smoky Mountains National Park and the University of Tennessee arboretum. M.S. Thesis, Univ. of Tennessee, Knoxville. 87 pp.

Van Driesche, R. G. and T. S. Bellows. 1996. Biological control. Chapman and Hall/ITP, New York, New York. 539 pp.

van Emden, H. F., V. F. Eastop, R. D. Hughes and M. J. Way. 1969. The ecology of *Myzus persicae*. Annu. Rev. Entomol. 14: 197-270.

Wallace, M. S. and F. P. Hain. 2000. Field surveys and evaluation of native and established predators of the hemlock woolly adelgid (Homoptera: Adelgidae) in the southeastern United States. Environ. Entomol. 29: 638-644.

Wallner, W. E. 1962. A field test with insecticides to control the scale, *Fiorinia externa*, on hemlock. Environ. Entomol. 55: 789-799.

Wallner, W. E. 1964. *Fiorinia* hemlock scale-pest of ornamental hemlock. Farm Res. 1:2-3.

Wallner, W. E. 1965. The biology and control of *Fiorina* hemlock scale *Fiorinia externa* Ferris. PhD Dissertation, Cornell University, Ithaca, New York. 166 pp.

Walters, W. E. 1956. Forest insect conditions in the Northeast-1955. U. S. For. Serv. Northeast. For. Expt Sta., Sta.79. 19 pp.

Wang, L. Y. 1986. Mass rearing and utilization in biological control of the lady beetle *Leis axyridis* (Pallas). Acta Entomol. Sinica. 29: 104.

Webb, J. W. 1977. The life history and population dynamics of *Acizzia russellae* (Hemiptera: Psyllidae). J. Entomol. Soc. So. Africa. 40: 37-46.

Webb, J. W. and V. C. Moran. 1978. The influence of the host plant on the population dynamics of *Acizzae russellae* (Hemiptera: Psyllidae). Ecol. Entomol. 3: 313-321.

Weiss, H. B. 1914. Notes on three imported insects occurring in New Jersey. Econ. Entomol. 7: 250-251.

Wells, M. L., R. M. McPherson, and J. R. Ruberson. 2001. Predation of parasitized and unparasitized cotton aphids (Homoptera: Aphididiae) by larvae of two coccinellids. J. Entomol. Sci. 36: 93-96.

White, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecol. 50: 905-909.

White, T. C. R. 1974. A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. Oecologia. 16: 279-301.

White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia. 33: 71-86.

Willard, J. R. 1974. Horizontal and vertical dispersal of California red scale, *Aonidiella aurantii* (Mask.) (Hemiptera: Diaspididae), in the field Aust. J. Zool. 22: 531-548.

Williams, J. R. 1971. Report Mauritius Sugar Indust. Res. Inst., no. 114. Mauritius.

Wilson, F.1960. A review of the biological control of insects and weeds in Australia and Australian New Guinea. Commonwealth Institute of Biol. Control, Tech. Comm. 1: 1-102.

Withycombe, C. L. 1923. Notes on the biology of some British Neuroptera (Planipennia). Trans Entomol. Soc. London, 1922: 501-594.

Yasumatsu, K. and C. Watanabe. 1964. A tentative catalogue of insect natural enemies of injurious insects in Japan — Part 1. Parasitoid-Predator Host Catalogue. Fukuoka, Japan: Entomol. Laboratory, Faculty of Agric. Kyushu Univ.

Young, J. A, C. D. Synder, J. Akerson, and G. Hunt. 1999. Assessment of landscape correlates of eastern hemlock decline due to hemlock woolly adelgid, pp. 134. In McManus, K.A., K.S. Shields, and D. R. Souto (eds.), Proc. Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, 22-24 June 1999, Durham, New Hampshire. U.S. Dept. of Agric., For. Serv., Durham, New Hampshire.

Yus, R. 1973. On the presence in the Iberian Peninsula of *Rhizobius lophanthae* (BlaiSDell 1892) (Col.: Coccinellidae). Graellsia. 29: 111-115.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey.

Vita

Christine A. Lynch grew up in Fort Lauderdale, Florida and graduated from Saint Thomas Aquinas High School in May 2000. Her interest in Entomology and Nematology began during her senior year in high school, when she began working at the University of Florida's the Fort Lauderdale Research and Education Center on nematodes in turfgrass. At the University of Florida in Gainesville, Florida, she began as a zoology major, but she became fascinated with insects after working with palm weevils during her second summer at the research center. She continued working at the center over the next couple of summers, and she worked with insect collections, termites, and white-footed ants. She graduated with a Bachelor of Science degree in Entomology and Nematology during June of 2004.

Next, she accepted an assistantship at the University of Tennessee under Dr. Paris Lambdin and began her research. During her degree, she gave numerous oral and poster presentations, and she received the Allen-Abrahamson Award for second place in the Master's Poster Competition at the North American Forest Insect Work Conference. At the Southeastern Branch meeting of the Entomological Society of America, she was chosen as the 2006 Photo Salon winner for the photomicroscopy section. She completed a Master of Science degree in Entomology and Plant Pathology with a concentration in Entomology at the University of Tennessee in Knoxville, Tennessee in December 2006. Christine is a member of Entomological Society of America, Gamma Sigma Delta Agricultural Honor Society, Florida Entomological Society, and Tennessee Entomological Society.